The ecology and behaviour of feral ferrets (*Mustela furo*) in Canterbury farmland, New Zealand.

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Craig Gordon Morley

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Abstract

Ferret (*Mustela furo*) control programs, especially those attempting to prevent the spread of *Mycobacterium bovis* (Tb), would greatly benefit from practical knowledge of ferret ecology and behaviour. This study had two main objectives: firstly, to investigate ferret ecology by examining ferret abundance, survival, trapping success, and diet; and, secondly, to investigate ferret behaviour and activity patterns by using an acoustically sensitive transmitter system (ASTS). Abundance and survival estimates of ferrets tagged with passive integrated transponders (PITs), showed a marked seasonal variation, and despite ferrets being controlled on one site, data from both sites showed that lagomorph numbers increased exponentially. A trapping success model (GLIM) showed that factors such as vegetation cover, rabbit sign, and animal tracks positively influenced capture rates. Although GPS technology provided accurate trap location data, trapping success also benefited from understanding the distribution signs of both predators and prey. GPS data further contributed to GIS models of animal movements, home range and site fidelity. As a result, trapping success was found to be affected by periods of low ferret abundance, fluctuations in trappability and possibly excess prey. It was found that, even though cats and ferrets use different hunting strategies, lagomorphs were their staple prey in North Canterbury. Unlike overseas habitats, New Zealand farmland lacks alternative suitable prey and this may explain the narrow diet of both predators. Even with the large increase in lagomorph numbers seen in North Canterbury in the second year of study, the diets of both predators remained the same, suggesting that these predators are unable to regulate lagomorphs once their numbers cross a certain threshold. By using ASTS technology to examine ferret behaviour and activity it was possible to identify a wider range of behaviours than previously documented using conventional radio tracking techniques. Despite using only one ferret, it was not only possible to document the time of an activity period, the length of each behaviour, as well as seasonal changes in activity, but also behaviours rarely recorded by researchers using more conventional techniques. Generally the ferret displayed an ultradian activity pattern, disputing the accepted nocturnal hypothesis. One implication for ferret control programs using baited traps was a documented decrease in eating behaviour during the breeding seasons. Nevertheless, this study provided as many questions as it did answers; however, with technology such as ASTS, further information about the behaviour and ecology of ferrets could advance future ferret control programs.

General Introduction

Ferrets (*Mustela furo* Linnaeus, 1758) belong to the Order Carnivora, Family Mustelidae. They are often confused with polecats (*Mustela putorius putorius*, L. 1758) as their morphological characteristics are almost identical (Ashton and Thomson 1955; Heptner 1964). Both polecats and ferrets have a long narrow body shape typical of all mustelids. Their most characteristic feature is a black mask around the eyes, while their fur is a light creamy colour and studded with long dark guard hairs, mostly along the flanks and legs (Sleeman 1989; Lavers and Clapperton 1990). Ferrets have a reputation of ejecting an odour from their anal sac as one form of communication (Clapperton *et al.,* 1988). Smell and hearing are a ferret's main senses, and they usually walk with their heads close to the ground sniffing and searching in holes and rabbit burrows.

The natural distribution of polecats in Europe ranges from the Atlantic coast in the west to the Urals in the east and from Scandinavia in the north to the Mediterranean in the south (Burton 1979). Polecats were introduced into Britain either by the Romans or Normans who domesticated and bred them for catching rabbits as well as for their fur (Marchington 1978; Wellstead 1981). The earliest known introduction of the domestic ferret was in 1867 (Fitzgerald 1964). Documentation from 1884 shows that almost 4000 ferrets were released into New Zealand, mainly in Marlborough (Thomson 1922). Ferrets now range throughout most of New Zealand; however, they are more likely to be found in low rainfall pastoral habitats that support high rabbit, *Oryctolagus cuniculus* and, hare *Lepus europaeus* numbers (Lavers and Clapperton 1990). It has been found that ferret abundance in New Zealand is often closely associated with rabbit abundance (Wodzicki 1950; Marshall 1963; Norbury and McGlinchy 1996).

Until the early 1990's, ferrets were largely ignored in agricultural circles. Indeed, many farmers saw them as an ally in their efforts to reduce rabbit numbers on their properties. However, Walker *et al.* (1993), in a survey of bovine tuberculosis (*Mycobacterium bovis*: Tb) in wild and feral animals, found 15.5% of ferrets necropsied (n = 84) had gross lesions of Tb. Subsequent surveys also confirmed a high prevalence of Tb in feral ferrets (de Lisle *et al.,* 1993; Cowan 1994; Ragg *et al.,* 1995). These results meant that feral ferrets could no longer be considered an ally of the farmer and they were declared as vectors of Tb (Ballard 1995). Although the likelihood of humans obtaining Tb from

livestock is small, Tb poses a threat to dairy, beef and venison exports worth over $5 billion/year (Blakeley 1993).

Prior to 1990, very few studies had looked at ferret behaviour and ecology in New Zealand. The first significant studies of ferrets concentrated on their general biology and distribution (McCann 1955; Marshall 1961; Marshall 1963; Fitzgerald 1964), home range (Lavers 1973; Moors and Lavers 1981), scent communication (Crump 1980; Clapperton 1989) and diet (Hurst 1974; Roser and Lavers 1976; Gibb *et al.,* 1978). Concern for many native species also involved research into the predatory habits of ferrets (Robertson 1976; Pierce 1987; Baker 1989). Although a vast wealth of knowledge was accumulated, more information on their behaviour and ecology was needed in light of the news that ferrets may be hosts for Tb.

Consequently, an extensive research programme was undertaken by various agencies to reveal more about feral ferrets. These studies have examined aspects of ferret ecology including: ferret denning behaviour and spatial organisation (Ragg 1997; Medina-Vogel 1998; Norbury *et al.,* 1998); secondary poisoning (Alterio 1996; Heyward and Norbury 1998); diet (Smith *et al.,* 1995; Ragg 1998); trappability (Moller *et al.,* 1996; Cross *et al.,* 1998); effects of ferret control on cattle reactor rates (Caley *et al.,* 1998); as well as Tb epidemiology (Lugton *et al.,* 1997a; Lugton *et al.,* 1997b; Caley 1998). In addition, studies of ferret behaviour, ecology and predatory impact not directly involved with Tb have also been carried out in recent years (Mills 1994; Middlemass 1995; Pascoe 1995; King *et al.,* 1996a; King *et al.,* 1996b; Norbury and McGlinchy 1996; Alterio *et al.,* 1997; Alterio and Moller 1997b; Alterio and Moller 1997a).

Although Tb is a major problem in cattle and deer, many farmers (especially sheep farmers) considered rabbits to be a greater threat to their livelihood than Tb. Farmers already plagued with high rabbit numbers (Gibb and Williams 1994; Parkes 1995), were worried that if ferrets (and cats) were removed from their farms, rabbit numbers would increase further as predicted by Barlow and Kean (1996). Furthermore, some conservationists were concerned that the wholesale removal of ferrets and cats would result in rats and stoats replacing them as predators of native species. From a conservation perspective, increases in rats and stoats could be more detrimental than ferrets and cats (Fitzgerald 1990b; Norbury and Murphy 1996). Thus, more research on predator/rabbit interactions was urgently required.

Mustelids are notoriously secretive and elusive animals that are rarely seen for long periods of time in the wild (Blandford 1987); therefore, gathering information on their behavioural ecology involves a substantial investment in time, money and technology. Unfortunately, for most studies this has not been possible. Trapping (either using capture-recapture techniques or kill trapping) and/or using conventional radio tracking equipment are the two most common methods of collecting information on ferrets in New Zealand. Trapping generally provides good ecological data on survival, recruitment, as well as abundance (Cross *et al.*, 1998), and radio tracking provides good information on the spatial patterns and movements of ferrets (Norbury *et al.*, 1998). However, information on their behaviour under natural conditions has been difficult to obtain.

1.1. Thesis Aims

The objective of this thesis was to investigate certain facets of ferret ecology and behaviour. Firstly, current methodology was used to investigate ferret population size and trapping success, as well as cat and ferret diets, while a new approach to conventional radio tracking was used to investigate ferret behaviour and activity patterns. My research on ferrets is presented in the next five chapters, and although these cover a range of topics, they pursue three main objectives:

i) to monitor and compare natural fluctuations in rabbit and predator populations between a control site and a treatment site where cats and ferrets were being removed;
ii) to obtain information about feral ferret behaviour, ecology and diet in North Canterbury, and;
iii) to examine how an acoustically sensitive transmitter system can be used to study the natural behaviour of ferrets.

1.2. Study Sites

The field component of the study was carried out on two coastal farms at Omihi, 80 km north of Christchurch, New Zealand (43°02'S., 172°59'E: Figure 1.1). Omihi was chosen for two reasons: a) its historical research importance and, b) because it was part of a larger study in North Canterbury examining the effects of ferret control on levels of bovine tuberculosis in cattle (Caley *et al.*, 1998).

Although the study sites were chosen for their similar topography, vegetation, and climate, minor differences existed between the two farms. *Cotswold,* consisting of a 507 ha core area that was bordered by a 500 m buffer zone to the north and west (Figure 1.2), was designated a non-treatment site to monitor the natural fluctuations of predators and prey. The buffer zone was used to alleviate neighbouring farmer's concerns about the release of ferrets that could potentially spread Tb. The second farm, *The Rock,* was 453 hectares with no buffer zone (Figure 1.3), and was used as a treatment site where all predators were removed after a six month mark-recapture study.

The two sites were separated by a ridge (approximately 400 m high and 1 km wide). Maps detailing the elevation and vegetation of *Cotswold* and *The Rock* are shown in Figures 1.4-1.5. These maps are important for illustrating the general layout of traps mentioned in the chapters on trap success and predator movements. Amuri limestone grading into glauconitic sandstone underlain by white calcareous mudstone were the main parent rock formations on both sites (NZ Geological Survey 1964). The soils were predominately Onepunga and Willowbridge yellow-grey to yellow-brown earth intergrades (Vucetich and Gibbs 1964). Both soil types were prone to drought conditions in summer and waterlogging in winter (Leamy and Fieldes 1976).

During the study, rainfall readings were taken 0.5 km away from *The Rock* and 1 km away from *Cotswold.* The mean annual rainfall over the period October 1995 to July 1997 was 958 mm. Previously, the 40 year average from the same location had been 981 mm (J. Little *pers. comm.*) During this study, measurable rain (> 0.1 mm) fell, on average, 118 days per year. Other meteorological data was taken from daily records measured at 0900 hours near Motunau, 5 km away from the study sites (National Institute of Water and Atmospheric Research 1998). During the study, the air temperature averaged 12.3°C and ranged from -4°C in June/July to 35°C January/February. Snow fell on five separate occasions, remaining on the ground for a only few days. The mean evaporation rate (> 0.1 mm) per month was 11.6 mm, while strong föhn winds (maximum during study: 106 kph) removed soil moisture in spring and summer.

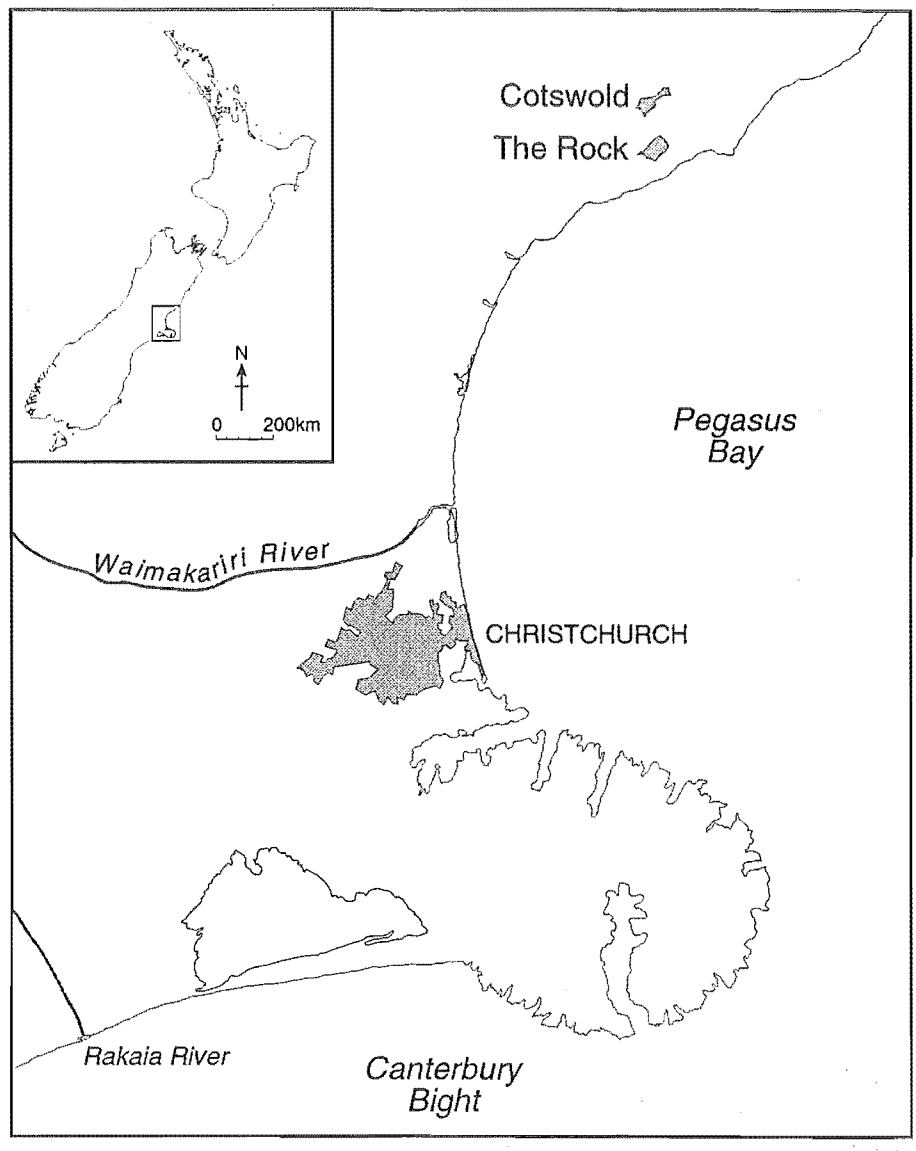


Figure 1.1. Location of *Cotswold* and *The Rock* from Christchurch, New Zealand.

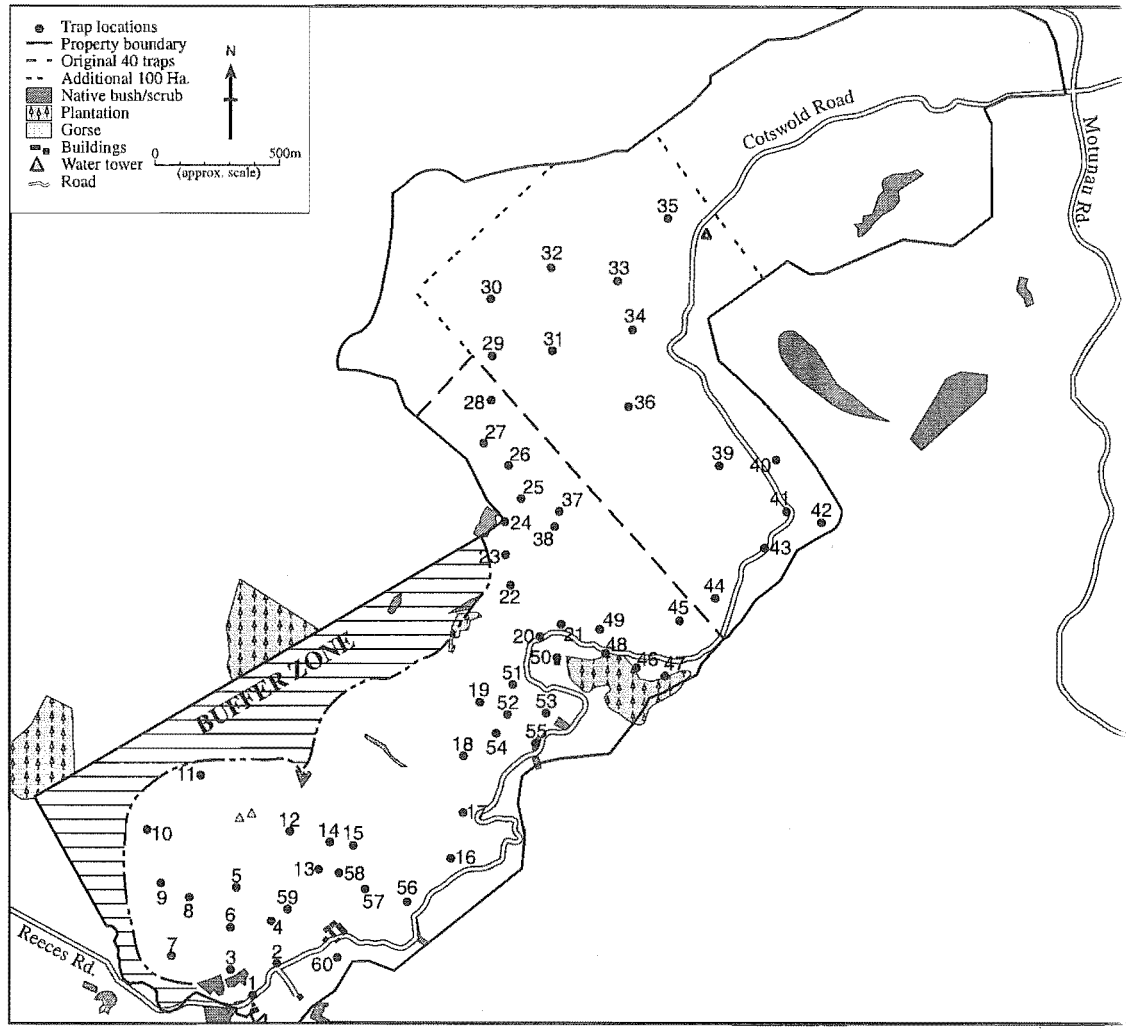


Figure 1.2. Map of *Cotswold* showing the buffer zone, plantations and layout of traps. The traps below the standard dotted line are the first 40 traps used from Oct-1995 to Sept-1996. The traps within the smaller dotted line area are the additional traps used from October 1996 to July 1997.

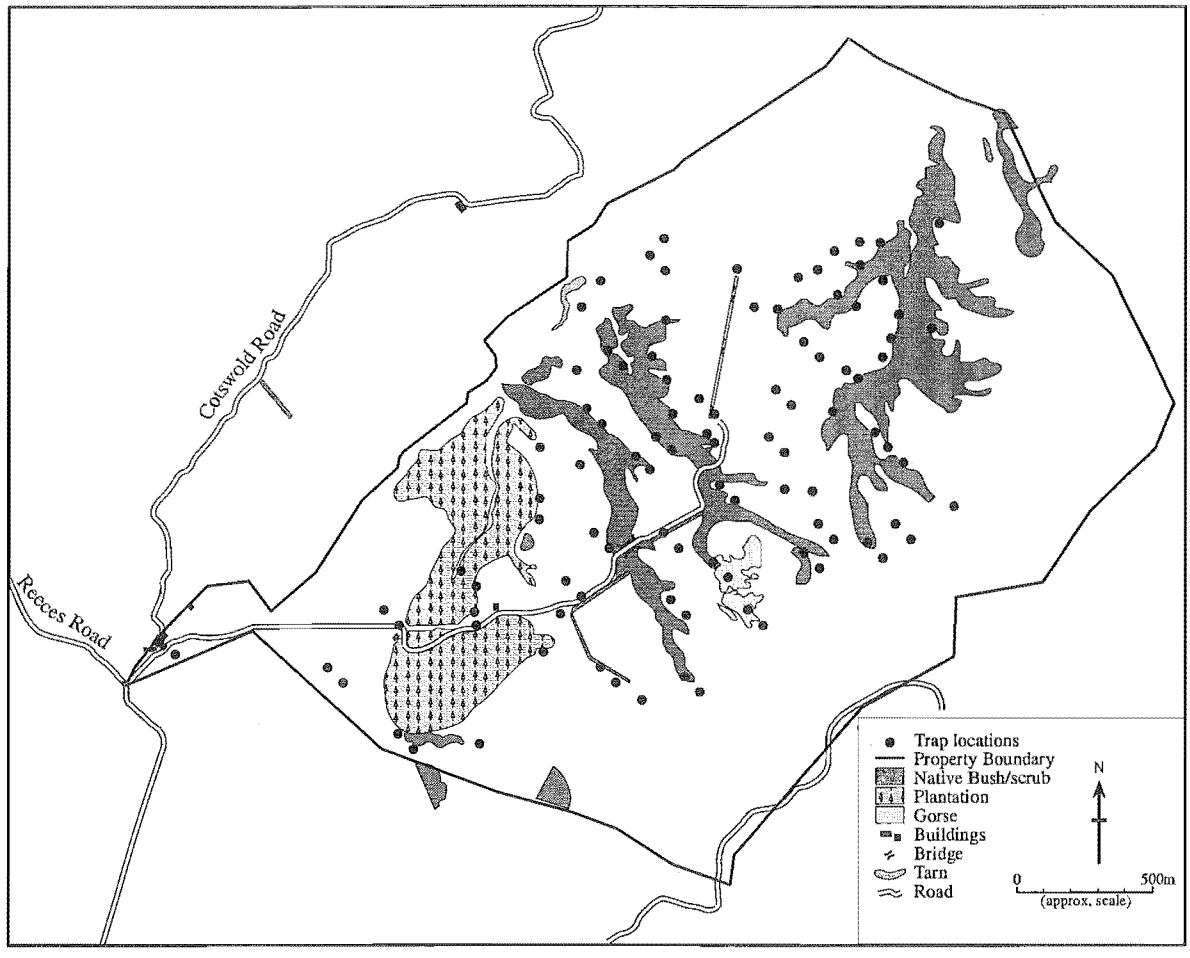


Figure 1.3. Map of *The Rock* showing plantations, gullies with native bush and all the various trap locations used. **Note:** the trap locations indicated are not permanent sites like that used on *Cotswold*.

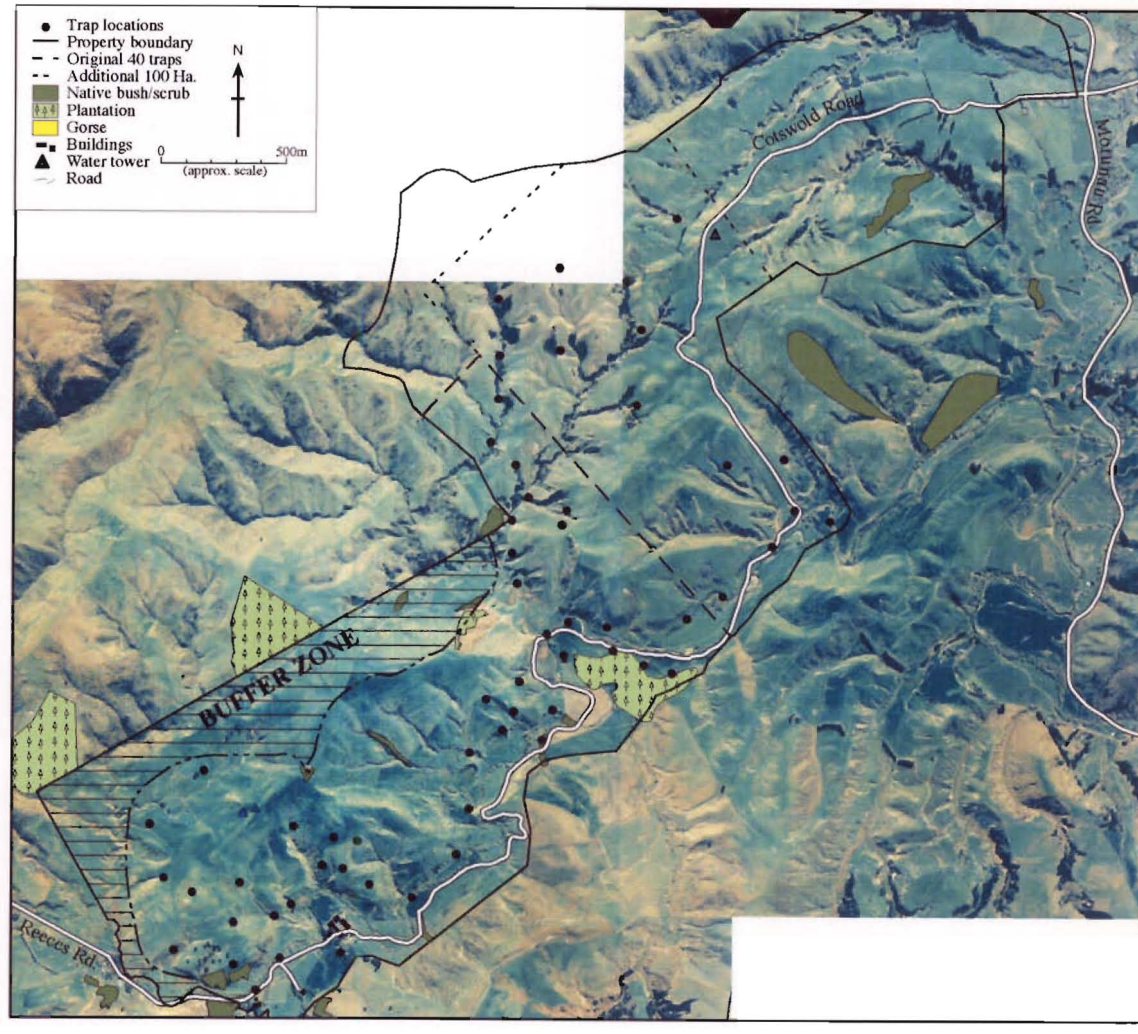


Figure 1.4. Aerial map of *Cotswold*, showing vegetation cover and location of traps. The traps below the standard dotted line are the first 40 traps used from Oct-1995 to Sept-1996. The traps within the smaller dotted line area are the additional traps used from October 1996 to July 1997.

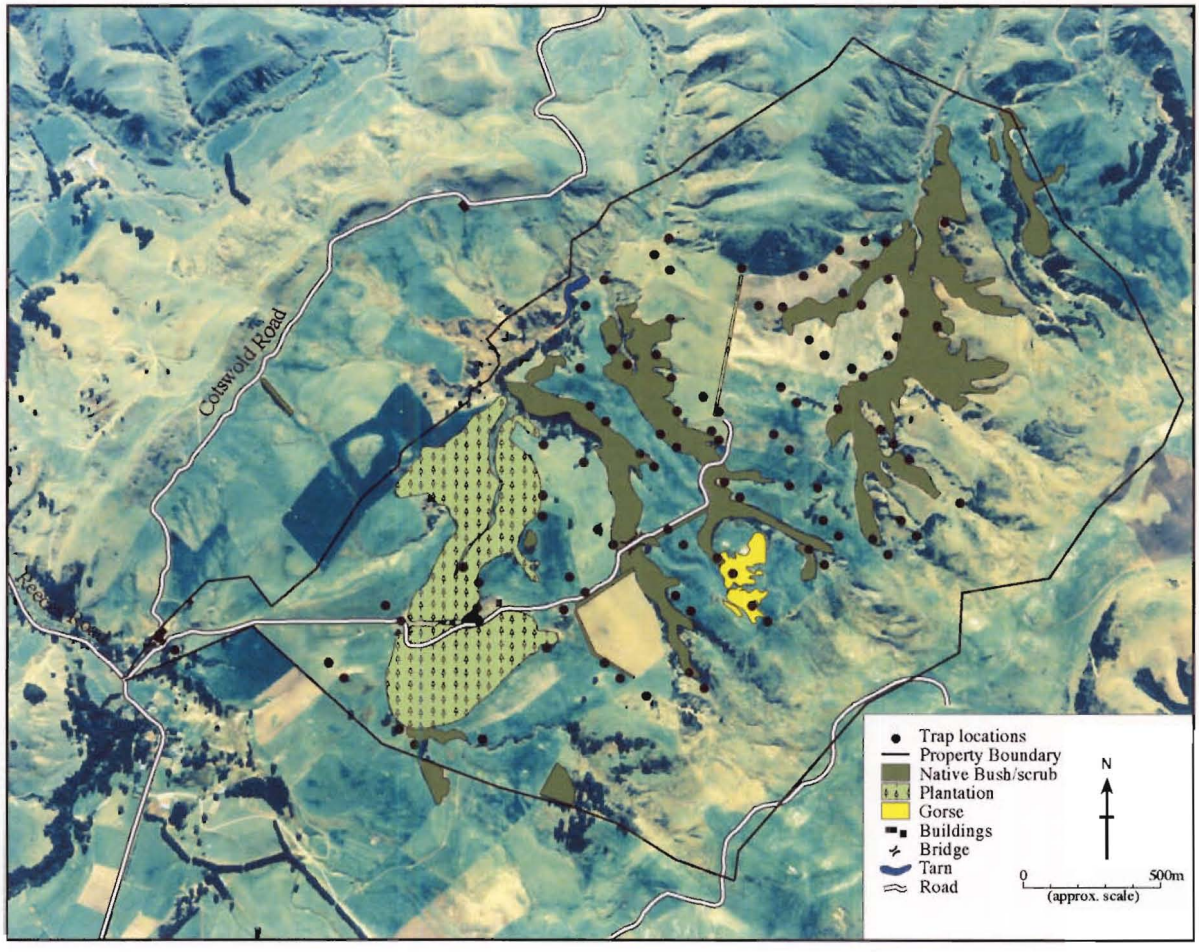


Figure 1.5. Aerial map of *The Rock*, showing vegetation cover and location of traps

1.2.1. Site biota

Domestic sheep (*Ovis aries*) and cattle (*Bos tauris*) were the main livestock on both farms. Other than the livestock and farm dogs (*Canis familiaris*), the most common vertebrate species identified at Omihi are shown in Table 1.1. No formal species abundance indices were measured, except for spotlight counts on rabbits and hares (see below).

a) Rabbits and hares

From 1974 to 1990, *The Rock* and two other farms were used in an experiment by the Ministry of Agriculture and Fisheries as non-treatment sites to test whether rabbit numbers stabilised in the absence of human control. Three nearby farms were simultaneously used as treatment sites where rabbits were shot (Bell 1990). Interestingly, rabbit numbers on the non-treatment sites remained relatively stable (Williams 1983). Because of this experiment no rabbits had been killed on *The Rock* for almost 20 years prior to my research. Predation (by ferrets and cats) and rainfall (drowning in burrows) were considered to be the primary mortality factors of rabbits in this area (Robson 1993). Additionally, no rabbits had been killed for at least 5 years on *Cotswold* even though it was not part of the above experiment. Prior to this study, rabbit numbers were low and stable (P. Reid, Canterbury Regional Council, *pers comm.*).

Although spotlight counts are unable to accurately measure rabbit and hare abundance (Frampton and Warburton 1994; Moller *et al.*, 1997), they are useful for comparing changes in lagomorph numbers (Fletcher *et al.*, 1999). At Omihi, rabbit and hare abundance was monitored each month at night by cruising on a 4WD quadbike travelling between 5-8 kph over permanently marked 10 km transects. I counted every lagomorph seen in a 100 m arc (using a 150 W spotlight mounted on a helmet) each kilometre.

All counts were carried out in fine weather, no cloud and little wind to minimise bias and decrease count variability. During the entire study no formal lagomorph control was undertaken on *Cotswold* but on *The Rock* lagomorphs were shot after autumn 1997. Rabbits were less intensively monitored on Tiromoana and Scargill than at Omihi, with rabbit counts carried out at 6 monthly intervals by the Regional Council. Because rabbits were only counted every six months by a different observer on Scargill and Tiromoana,

Table 1.1. Feral and wild species seen, heard or trapped at Omihi.

Class	Possible Prey	Seasonal Availability (Breeding Season)
Osteichthyes		
	Longfinned eel (*Angilla dieffenbachii*)	All year[1]
	Shortfinned eel (*Anguilla australis*)	All year
	Common river galaxias (*Galaxias vulgaris)*	All year
	Common bully (*Gobiomorphus cotidianus)*	All year
Amphibia		
	Common skink (*Oligosoma nigriplantare polychroma*)	All year (Jan-Feb[2])
	Gecko (*Haplodactylus maculatus*)	All year (Feb-May)
	Frog (*Litorea raniformes*)	All year (Apr-Dec)
Aves		
	White-backed magpie (*Gymnorhina tibicen hypoleuca*)	All year (Aug-Nov)
	Song thrush (*Turdus philomelos*)	All year (Jun-Jan)
	Blackbird (*T. merula*)	All year (Jul-Jan)
	Starling (*S. vulgaris*)	All year (Sep-Jan)
	Paradise shellduck (*Tadorna variegata*)	All year (Aug-Jan)
	Spur-winged plover (*Lobibyx novaehollandiae*)	All year (Jul-Dec)
	Welcome swallow (*Hirundo tahitica*)	All year (Sep-Feb)
	Skylark (*Alauda arvensis*)	All year (Oct-Jan)
	Fantail (*Rhipidura fuliginosa*)	All year (Aug-Jan)
	Silvereye (*Zosterops lateralis*)	All year (Aug-Feb)
	Yellowhammer (*Emberiza citrinella*)	All year (Oct-Jan)
	House sparrow (*Passer domesticus*)	All year (Jul-Apr)
	Australasian harrier (*Circus approximans*)	All year (Oct-Dec)
Mammalia		
	Rabbit (*Oryctolagus cuniculus*)	All year (Aug-Apr)
	Hare (*Lepus europaeus*)	All year (Aug-Feb)
	Mice (*Mus musculus*)	All year (Sep-Apr)
	Rat (*Rattus norvegicus* and *R. rattus*)	All year (Sep-Apr)
	Pig (*Sus scrofa)*	All year (Sep-Apr)
	Hedgehog (*Erinaceus europaeus*)	All year except Jun-Aug (Oct-Feb)
	Possum (*Trichosurus vulpecula*)	All year (Sep-Apr)

1) Seasonal availability: All year = these animals were present in all four seasons, however, this does not mean they were equally abundant all year round.

2) Breeding season (in parentheses): Typical reproductive and development period.

this information was not used in my study.

i) *Rabbit abundance*

For the first six months of the study, when no predator control was implemented on either site, rabbit numbers increased by 3-fold (Figure 1.8). After predator control was implemented on *The Rock* rabbit numbers on both sites continued to gradually increase at the same rate but after six months (October 1996) rabbit numbers increased dramatically. A 34-fold increase occurred on *The Rock* from 53 rabbits per 10 km (R/10 km) in October 1995 to 1793 R/10 km in April 1997. Similarly, on *Cotswold* rabbit numbers increased by 36-fold from 22 R/10 km in October 1995 to 804 R/10 km in July 1997 (Figure 1.8). Although *The Rock* had more rabbits per 10 km than *Cotswold* no significant difference was found between the proportional rate of increase in rabbit numbers between sites (paired *t-test* = 0.48, d.f. = 18, $p = 0.635$).

ii) *Hare abundance*

In contrast with the rabbit population, hare numbers were higher on *Cotswold* than on *The Rock*. For the first six months of monitoring hare numbers on *Cotswold* increased by 26-fold but on *The Rock* only a 4-fold increase was observed (Figure 1.8). Even after predator control began on *The Rock,* hare numbers remained relatively stable but a 2-fold increase was observed after summer 1997. Hare numbers on *Cotswold* increased after autumn 1996 and fluctuated around 50 hares per 10 km until they too doubled their number after autumn 1997. However, unlike the rabbit population, the proportional rate of increase of hares on *Cotswold* was significantly different to that on *The Rock* (paired *t-test* = 2.48, d.f. = 18, $p = 0.023$).

b) Vegetation

The dominant pasture species were *Agrostis capilaris, A. tenuis, Cynsurus crisalus, Holcus lanatus, Trifoilum* spp. and *Lolium* spp. *Kunzea ericoides* (kanuka), *Leptospermum scoparium* (manuka), *Cordyline australis* (cabbage tree), *Discaria toumatou* (matagouri), *Festuca novae-zelandiae* (tussock), *Ulex europaeus* (gorse) and *Cytisus scoparius* (broom) were the main scrub species found in the gullies and on many of the hills. *Salix* spp. (willow) grew along the Motunau Stream which ran through *Cotswold*, while several large remnant patches of *Nothofagus solandri* (black beech) grew on *The Rock.* In the wetter areas surrounding the tarn on *The Rock* and around the small ponds on both properties,

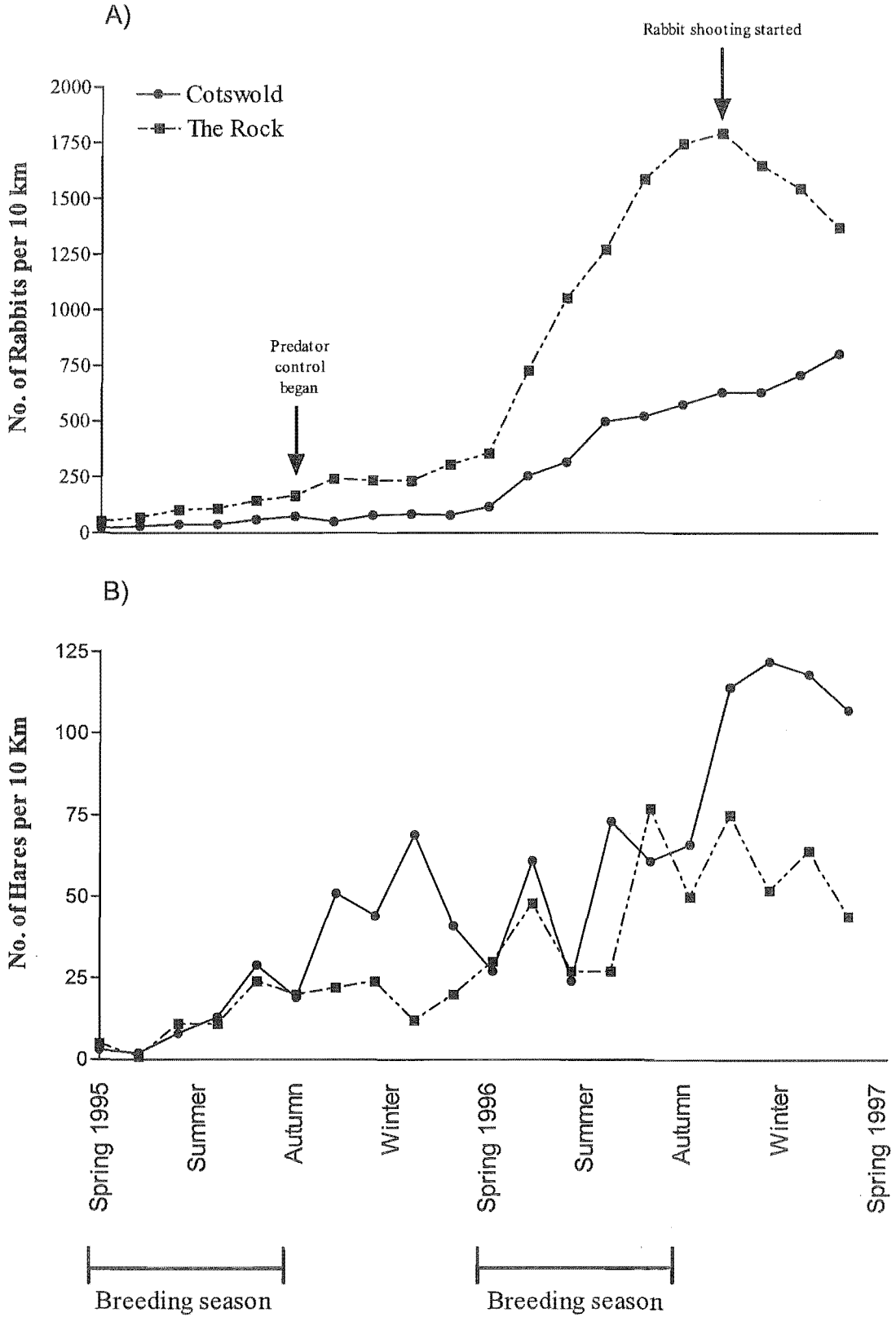


Figure 1.8. Changes in rabbit and hare abundance on *Cotswold* and *The Rock* from Spring 1995 to Spring 1997 before the release of RCD in September 1997. Figure A) number of rabbits counted and B) the number of hares counted, over a 10 km transect.

Juncus spp.(rushes) was the most common species present. *Pinus radiata* (pine) was planted to create plantations and shelterbelts along some of the fencelines, as well as in the gullies.

1.3. Research Questions and Objectives for each chapter

1.3.1. *Chapter Two*

New Zealand is thought to have the largest feral ferret population in the world (Nowak and Paradiso 1983) although no recent census estimates are available. The first objective of this chapter is to estimate the abundance, survival and recruitment of ferrets found in a pastoral area (500 ha) of North Canterbury, considered to be typical of many lowland farming areas of New Zealand. The second objective of this chapter is to assess the durability and efficiency of two commonly used marking systems (passive integrated transponders and ear tags) and to ascertain whether their use resulted in any undue bias.

1.3.2. *Chapter Three*

Trapping is both labour intensive and time consuming, yet it is still the most efficient method of removing ferrets as well as providing a reliable index of ferret abundance (Cross *et al.,* 1998). One question constantly asked by researchers and farmers alike is: *what are the main factors that affect trap success*? The first objective of this chapter is to assess both biotic and abiotic factors affecting capture rates, while the second objective is to consider the use of trapping in examining the spatial distribution, movement and site fidelity of ferrets.

1.3.3. *Chapter Four*

Ferret and cat diet has been the subject of many studies in New Zealand for various reasons (Lavers and Clapperton 1990; Fitzgerald 1990a); most have concluded that these predators predominately eat lagomorphs (Langham 1990; Smith 1994; Ragg 1998). Yet, outside of New Zealand this low diversity of prey consumed is not always apparent. The objective of this chapter is to compare data obtained from cat and ferret diets in North Canterbury to those of cats on islands and in Australia as well as polecats in Europe. It also examines whether cats and ferrets in New Zealand have narrow or broad diets..

1.3.4. *Chapter Five*

Radio tracking is commonly used to investigate an animal's home range, movements and physiological state (Cochran 1980; Kenward 1987). However, unless the animal can be viewed directly, conventional radio tracking signals provide only limited data on its behaviour and activity patterns (Greager *et al.,* 1979). As Blandford (1987) points out, in his review of polecat literature, a lot of information on polecat behaviour has been by "speculation in the absence of facts", thus, a new approach is required.

The objective of this chapter is to examine a methodology that allows a researcher to not only hear the vocalisations and activities of an animal, but also to describe them. This was done by using an acoustically sensitive transmitter system (ASTS) in two-stages. Firstly, the sounds and vocalisations made by a ferret wearing an ASTS collar were simultaneously recorded with video footage of its activities and behaviours in an observation enclosure. A library of sounds was then documented and classified into known behaviours. The second stage involved using this library to calibrate known sounds and vocalisations to certain activities and behaviours of a ferret wearing an ASTS collar in a much larger enclosure where it could not be viewed. This chapter also describes the advantages and limitations of ASTS technology in examining animal behaviour.

1.4.5. *Chapter Six*

The objective of Chapter 6 is to use the ASTS technology, described in Chapter 5, to identify reasons why ferrets are difficult to trap during the breeding season. This question was a direct result of issues raised in both Chapters 2 and 3, as well as the work of Ragg (1997), who found a pronounced decline in the trappability of ferrets during the breeding season. Several hypotheses have been proposed to explain the lack of trap success over the breeding season; however, this thesis is the first to address the question directly. In addition, Chapter 6 also examines activity patterns and activity types in ferret behaviour.

Chapter Two

Analysing ferret abundance, survival and recruitment in North Canterbury, New Zealand using passive integrated transponders and ear tags

2. Abstract

At present in New Zealand, robust estimates of ferret (*Mustela furo*) abundance and survival are rare. Capture-recapture techniques, using identification tags, are currently the most common method for gathering data on ferret abundance and survival; however, a crucial assumption of capture-recapture models is that animals do not lose their tags so they can be positively identified. In this study, ferrets were trapped in 16 sessions over a 22 month period and then marked with both passive integrated transponders (PITs) as well as ear tags. The data gathered from recaptures were evaluated using a Jolly-Seber model to quantify any bias associated with their use. It was found that PITs provided more accurate estimates than did ear tags but they also cost substantially more; however, as only six percent of ferrets lost their ear tags, ear tags remain a viable identification method for short term abundance and survival studies. The data also showed that ferret capture rate varied seasonally; higher during the summer to autumn period, and lower during the winter to spring, especially during the breeding season. This breeding season decline in capture rate was considered to be a result of both low ferret abundance as well as reduced trappability.

2.1 Introduction

Ferrets (*Mustela furo*) are known to spread bovine tuberculosis (*Mycobacterium bovis*: Tb) to livestock and threaten endemic wildlife in New Zealand (Alterio and Moller 1997b; Caley *et al.*, 1998). Trapping is the most widely used technique to monitor and control ferret populations (Cross *et al.*, 1998), but intensive trapping of ferrets in North Canterbury over four years failed to show any significant reduction in the number of ferrets remaining (Caley *et al.*, 1998). Trapping is expensive and time-consuming, therefore, reliable abundance estimates are required to determine the efficacy of control and the most appropriate time to trap ferrets (Moller *et al.*, 1996). Interestingly, there are few or no published robust data on ferret abundance and survival in New Zealand. Yet, this information is essential for landholders and conservation managers to develop control strategies and epidemiological models (Ragg 1997).

Ferret trapping is very seasonal with most ferrets caught in summer and autumn, and only a few ferrets captured in winter and spring (see Chapter 3). The low catch rates during winter and spring are a function of both density and of the trappability of ferrets (Moller *et al.*, 1996; see Chapter 3). Mustelids, such as stoats (*Mustela erminea*), can be difficult to trap because they are wary and intelligent and, usually live at low densities (King 1989; see Chapter 3). Trapping rates of mustelids can also vary according to the densities of their prey. For example, fewer ferrets were captured when there was a proliferation of young lagomorphs in late winter and spring than in summer and autumn (Norbury and Heyward 1996), and relatively more stoats were captured when their main prey (mice; *Mus musculus*) became scarce (Alterio *et al.*, 1999).

Capture-recapture (CR) procedures use repeated sampling techniques to investigate the dynamics of a mobile animal population. Capture histories of marked animals are then used to obtain estimates on abundance, recruitment and survival (Pollock *et al.*, 1990). However, estimates from such CR experiments often assume the population is closed to additions and deletions which is incorrect. Open population models such as the Jolly-Seber model allow for additions and deletions provided the following assumptions are applied: 1) all marked ferrets present have the same probability of capture; 2) that marked animals have the same probability of survival as unmarked animals; 3) all samples are instantaneous and each release is made immediately after the sample; 4) that trapping and

marking does not alter the animal's behaviour or chances of recapture; 5) that animals do not lose their marks; and 6) all marks are recorded correctly on every sampling occasion (Pollock *et al.,* 1990; White *et al.,* 1982).

Perhaps the most commonly used method for marking small mammals in CR studies are externally attached tags, particularly ear tags (Twigg 1975). If the external tags cannot be read from a distance, the animal has to be repeatedly trapped and handled in order to be identified, and this may affect its recapture probability. Hungry animals may become trap-happy or nervous ones trap-shy, after the process of capture and marking (Begon 1979). Although natural capture heterogeneity is likely due to individual differences in age and sex (i.e., juvenile male mustelids are more likely to be trapped than adult females; Buskirk and Lindstedt (1989), additional sources of capture heterogeneity should be reduced in order to minimise bias (Pollock *et al.,* 1990; Seber 1986).

Tag loss is crucial in CR studies because if animals lose their tags and cannot be identified then the estimated recapture rates will be negatively biased, and depending on the CR model used, this may cause the survival rates to be underestimated and the population values to be overestimated (Arnason and Mills 1981; Manly 1971). In addition, failure to record all marked tags correctly will result in an overestimation of the population size (Otis *et al.,* 1978; Seber 1973). Therefore, reducing tag loss can improve the accuracy and precision of CR results (Seber 1986). Unfortunately, many externally placed tags are easily lost (Barrowman and Myers 1996; Testa and Rothery 1992).

Passive integrated transponders (PITs) are an alternative method for identifying animals (Elbin and Burger 1994; Harper and Batzli 1996; Schooley *et al.,* 1993). A PIT tagging system consists of small, injectable, glass-encapsulated microchips (transponders with a unique alphanumeric ID code). It has electromagnetic coils which work in conjunction with a compatible mini portable reader (MPR). The transponders are implanted into an animal and remain inactive until read with an MPR. Once implanted, the transponder generally remains with the animal for life (Becker and Wendeln 1997). PIT identification codes can be read without handling the animal, as the MPRs generate a magnetic field across a distance of 30 cm, activating the transponder to transmit the unique ID code (Fagerstone and Johns 1987).

Very few robust data are available on ferret abundance and survival in New Zealand. Therefore, the aim of this chapter is twofold: 1) to estimate ferret abundance,

recruitment and survival on farmland in North Canterbury, New Zealand, and 2) to assess the durability and efficiency of two commonly used marking systems (ear tags and PIT tags) in the field and to quantify any bias associated with their use.

2.2 Methods

2.2.1. Study areas

The study area was located on farmland 80 km north of Christchurch, New Zealand (43°02'S., 172°59'E), situated 3 km west of the coastline. This area was chosen because of reported stable populations of lagomorphs and predators (Bell 1990; Robson 1993). For a full description of the *Cotswold* study site refer to Chapter 1.

2.2.2. Population Monitoring

a) Trapping Procedure

The aim of the CR programme was to estimate ferret abundance and survival over a 500-600 ha area of pastoral farmland. Ferrets were caught in wire cage traps baited with fresh rabbit meat. Bait was replaced daily in the summer and every second day in winter. Each trapping session was six consecutive nights and all traps were checked daily. In all, there were 16 trapping sessions over a 22 month period (Table 2.1). Most trapping sessions were in consecutive months during the summer but unfortunately during the winter climatic and logistical constraints only permitted trapping every second month.

Although not directly part of my study, ferrets in the buffer zone (see Chapter 1) and on the neighbouring farms were also trapped. These ferrets were killed by farmers during two main periods (Table 2.1) as part of a bovine tuberculosis (*Mycobacterium bovis:* Tb) control programme. Many of the neighbouring farmers, aware of this study, set traps on or near the boundary of the study site. Consequently many tagged ferrets were killed but the farmers did provide details on where and when a ferret was captured. With this additional information I was able to take into account both live recaptures and dead recoveries. Therefore, the trapping sessions have been divided into 4 survival periods, herein after referred to as S_1—S_4 (Table 2.1).

Table 2.1. The sixteen trapping sessions divided into four survival periods (S). The survival periods resulted as part of the Omihi Tb control programme when farmers on adjacent properties trapped and killed ferrets, including those tagged in this study.

Date of trapping session	Survival period (S)
16-22 Oct 95	1
11-17 Oct 95	1
15-21 Jan 96	1
12-18 Feb 96	2
11-17 Mar 96	2
15- 21 Apr 96	2
10-16 Jun 96	2
12-16 Aug 96	3
14-20 Oct 96	3
13-19 Jan 97	3
10-16 Feb 97	3
10-16 Mar 97	4
14-20 Apr 97	4
12-18 May 97	4
16-22 Jun 97	4
14-20 Jul 97	4

Forty traps were used in periods S_1—S_2 and 60 traps were used in periods S_3—S_4. The extra 20 traps were set in an additional 100 ha. The traps were spaced at 150-500 m intervals and were placed in locations where they were likely to catch ferrets (see Chapter 3). Once captured, each ferret was transferred to a small see-through crush-bag. Within the crush-bag the ferret was rendered immobile so it could be easily sexed, aged (using its sagittal crest and teeth) and, given tags without the need for anaesthetics or clumsy gloves. For further details of the trapping protocol and layout refer to Chapters 1 and 3.

b) Tagging

To tag and identify the ferrets I used Monel ear tags (National Band and Tag Company Newport, USA, size 1005, style 49) and PIT tags (Destron-Fearing, St Paul, USA). Tag loss (both ear and PIT) was assumed to be the same for all ferrets regardless of age or sex.

I used several criteria to test the durability and efficiency of the ear tags. After capture, each ferret was examined for an existing ear tag. To exclude the possibility of an incorrect attachment, a ferret was deemed to have lost an ear tag only if the ear pinna was torn in a V-shape. Secondly, I assessed the time it took to implant a PIT tag and apply ear tags to both ears. Thirdly, I noted the time it took to read an ear tag and PIT tag upon recapture and, finally, I assessed the accuracy of recording tag numbers. To record the accuracy and efficiency of the two systems, the left ear tag (if present) was read first, then the ferret was scanned for its PIT tag and finally the right ear tag was read. The time it took to place the ferret into the crush bag was omitted from this test. Although PIT and ear tag data were manually recorded into a notebook on location, the PIT information was also stored in the MPR scanner and accessed later when tag accuracy was being compared.

Each PIT tag applicator was used only once and then discarded. Thus, only factory sharpened applicator needles were used, to reduce trauma and the spread of any disease. To prevent ferrets from biting the transponders, PIT tags were implanted subcutaneously between the scapulae, following the recommendations of Fagerstone and Johns (1987) and Harper and Batzli (1996). To reduce handling time no anaesthetic was used. Although no sutures were required, an adhesive (Vetbond®, 3M) was applied to the puncture wound to prevent the PIT tags escaping from the injection site (Seebeck and Booth 1996). All transponders were tested before and after implantation.

Ninety-eight ferrets (Table 2.2) were used in the CR study; the 84 new ferrets captured on *Cotswold* and an additional 14 ferrets I translocated from *The Rock* to

Cotswold. The additional 14 ferrets were part of a concurrent study on ferret homing ability (see Chapter 3). To help evaluate the performance of the tags only those ferrets which received both PIT tags and ear tags were used to test tag retention. Only the first 84 ferrets captured were given PIT tags. The first 12 ferrets captured were only tagged with one ear tag and one PIT tag but two of these ferrets lost their ear tags within the first month so all ferrets after this received two ear tags, one on each ear. If a ferret was observed to have lost an ear tag between captures it was given a new ear tag and its records were updated.

To estimate the proportion of ferrets losing tags over the study period the number of marked ferrets in the recapture sample were designated R_A (A = ear tags), R_B (B = PIT tags) and R_{AB} (AB = both ear and PIT tags). Of those ferrets which kept mark A, the fraction losing B equals R_A/R_{AB} and vice versa.

c) *Population abundance and survival analysis*

Only data from *Cotswold* was used to estimate the abundance and survival of ferrets. The standard Jolly-Seber model was used in the programme JOLLY™ to enumerate ferret abundance, recruitment and survival (Pollock *et al.*, 1990). This population model allows for additions and deletions from the catchable population (Jolly 1965; Seber 1965). To account for any edge effects, the area considered to be covered by the trapping grid was extended at the edge by half the average home range length (see Kenward 1985). Ferret density was estimated by taking the new extended area and dividing this by the estimated number of ferrets calculated in programme JOLLY. Because a further 100 ha was added to the trapping grid in periods S_3 and S_4, all estimates of density were calculated using the extended trapping area for these sessions.

Because of insufficient movement data and potential problems associated with low sample size during some trapping sessions, the mean home range length and JOLLY estimates were not separated by sex. The hypothesis that the distribution of recaptures (equal probability of capture) is constant was supported in this study ($\chi^2 = 6.38$, d.f. = 9, $p = 0.70$). To compare the degree of accuracy and precision of the two marking systems, ferret density, survival and recruitment estimates were calculated twice. Firstly, from the PIT capture data and, secondly, from the ear tag capture data. The JOLLY estimates in

Table 2.2. Summary of tags given to ferrets.

	Male	Female	Total
Number of ferrets caught	57	41	98
Received one ear tag and a PIT tag	7	5	12
Received two ear tags and a PIT tag	39	31	70
Received only two ear tags	10	6	16
Lost an ear tag	8	12	20
Lost a PIT tag	1	0	1
Number of recapture occasions	157	105	262

Figure 2.1 were computed using the mean ± 1 standard error of the mean (SE($\bar{x}$)).

Although the Jolly-Seber model can produce negatively-biased estimates of population abundance due to differences in capture probability (Seber 1986), it gives a more precise estimate of ferret survival and abundance. Furthermore, it is the only model that has been consistently used by other ferret researchers in New Zealand, therefore its estimates are useful for comparative reasons.

Programme MARK™ was used to estimate ferret survival via numerical maximum likelihood techniques. Using the joint live and dead model developed by Burnham *et al.*, (1995), the parameters selected in the model were S(i) survival rate (survival probability of the marked ferrets), p(i) recapture rate (probability of capture), r(i) reporting rate (tag reporting rate) and F(i) fidelity (probability that the animal remained in the study area and was available for capture). Model outputs are arranged in order. The most important factor in selecting the models for mark-recapture survival inference were the differences between $QAIC_c$ (quasi-Akaike's Information Criterion $_{corrected}$) values (i.e., $\Delta QAIC_c$). Therefore, the model that selects the smallest $\Delta QAIC_c$ with a biologically meaningful number of parameters is regarded as the best fitting model (Burnham *et al.*, 1995; Lebreton *et al.*, 1992).

2.3. Results

2.3.1. Tag Evaluation

Of the 98 ferrets captured for the first time that were marked and released, 69 were recaptured on 262 occasions (Table 2.2). A total of 184 ear tags were attached to the ferrets. Twenty ear tags were recorded missing from 15 ferrets, hence, estimated ear tag loss was 11%. One ferret lost 3 ear tags at different times, one ferret lost two ear tags at different times and one ferret lost both ear tags between consecutive trapping sessions. Four ferrets lost their only ear tag, two within the first month of trapping. Five ferrets which lost their ear tags could be identified only from their PIT tags. Had the study only relied on ear tags, then 6% of all ferrets would have been unidentifiable, with up to 24% unidentifiable if only one ear tag had been used. Using PIT tags in the field resulted in all ferrets being identifiable

Several differences were evident when comparing the JOLLY estimates between the two tagging systems (Figure 2.1). First, PIT tags provided lower a standard error and

narrower confidence interval than ear tags. Second, although precision and bias were different, the parameters estimated using JOLLY for both tagging systems were similar, that is, there was substantial overlap in the standard errors between PIT tags and ear tags. This is probably because only 6% of ear-tagged ferrets would have been unidentifiable had PITs not been used. Nevertheless, abundance was overestimated using ear tags in periods S_1—S_2 and survival was underestimated in periods S_3—S_4. Recruitment estimates were only slightly affected, as the standard error of ferrets recruited using ear tag data was marginally larger than the PIT tag data (see Figure 2.1d).

Ear tag retention, from the date of first capture to the date of last capture, ranged from 1 day (when a ferret was recaptured the following day without an ear tag) to 431 days. Mean ear tag retention over the study was 85.7 days (SE = 11.8, n = 69). Of all the ferrets which lost their ear tags, all but one also lost a substantial part of their ear pinnae. Torn pinnae were recorded in 8 out of 207 recaptured ferrets, excluding those which had lost ear tags already. Proportionately, more female ferrets (29%) lost at least one ear tag during the study than males (14%) although this difference was not significant ($\chi^2 = 3.41$, d.f. = 1, $p = 0.065$).

On 9 out of 262 recapture occasions (3.5%), an ear tag number was misread. This was due to some numbers appearing similar if marked or dirty (e.g., 0 and 8, 1 and 7). The additional scanning of PIT tags helped me to correct this potential error. The mean time it took to read the ear tag(s) was much longer ($\bar{x}$ = 43 seconds, ± SE = 0.96) than using the MPR scanner (<5 seconds). The time it took to implant a PIT tag using no anaesthetic was approximately the same it took to attach both ear tags (2 minutes).

Nineteen tagged ferrets were captured and killed by farmers plus 27 untagged ferrets (Table 2.3). Of the nineteen, one ferret, after losing both ear tags, could only be identified by its PIT tag, with an additional four ferrets losing at least one ear tag. The remainder retained both their ear tags, while all but one had functional PIT tags. The ferret with the non-functional PIT tag had previously been caught twice in quick succession and the PIT tag had given a reading on the MPR scanner on each occasion. One possible reason for non-functional PIT tag was that the farmer killed the ferret with a blow to the head, which then broke the PIT tag. Of the nineteen ferrets killed by farmers, twelve were necropsied by

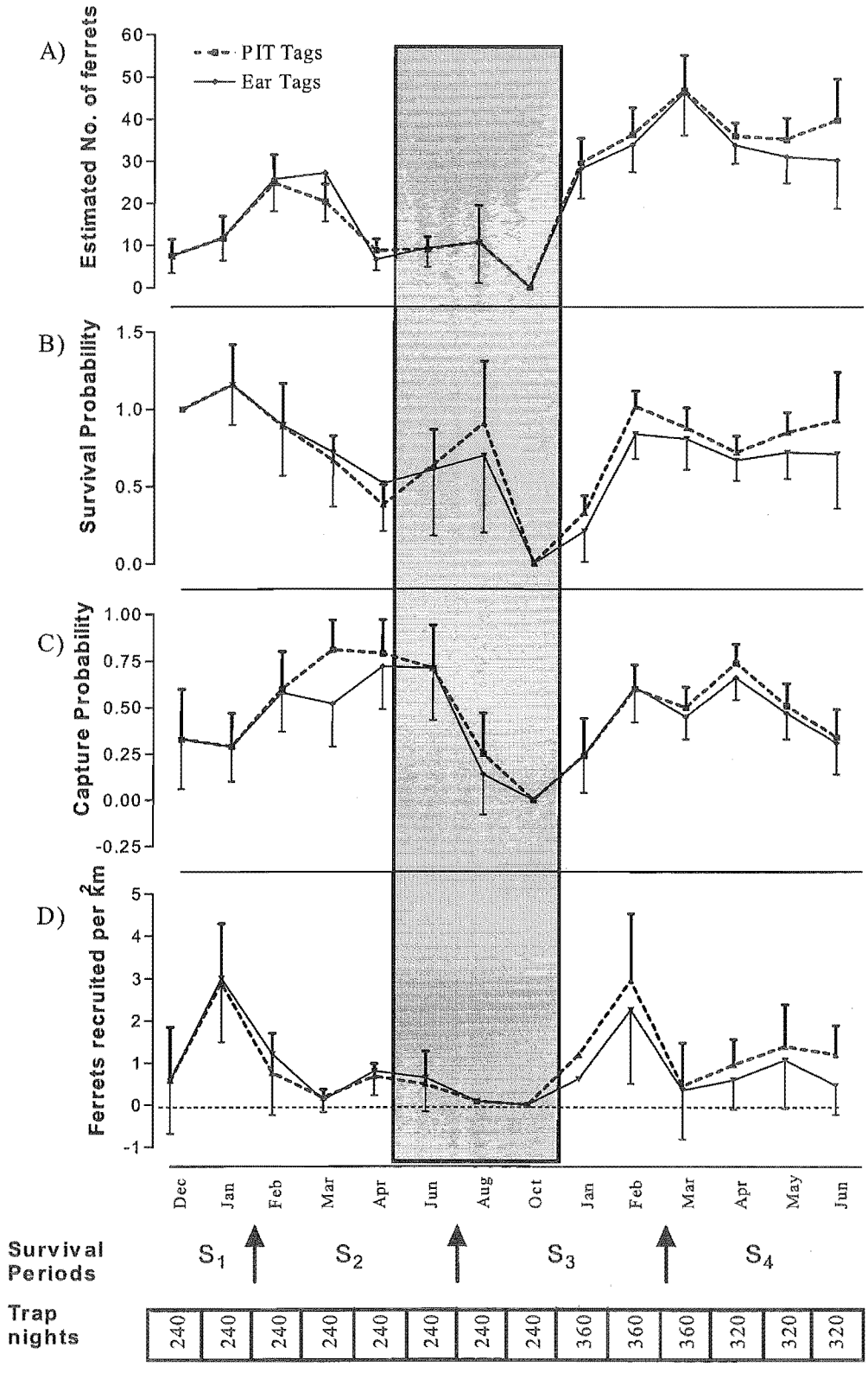


Figure 2.1. Ferret abundance (A), survival (B), capture probability c) and recruitment (D) estimates from programme JOLLY for PIT tags and ear tags on *Cotswold* from December 1995 to June 1997. Also shown are the number of trap nights and the four survival periods (S_1-S_4). Means ± SE above dotted line = PIT tags and, means ± SE below solid line = ear tags. White area = monthly trapping periods, shaded area = bimonthly trapping period.

Table 2.3. Number of ferrets trapped and killed by farmers either on *Cotswold* or on the immediate boundary of *Cotswold*.

Ferrets	Feb-Jun 96	Mar-Jul 97	Total
Tagged	11	8	19
Not tagged	18	9	27
Total	29	17	46

myself for Tb. During necropsy, each PIT tag was located amongst the fibrous connective tissue and found to be fully functional. No migration of the PIT tags was evident. The seven remaining ferrets were not examined for their PIT tags as their carcasses were sent to a veterinarian for Tb necropsies.

2.3.2. Abundance and density estimates

Ferret abundance and density estimates are shown in Table 2.4. From the JOLLY estimates using ear tag data for periods S_1 and S_2 (refer to Table 2.1), the population density of ferrets peaked in February 1996 at 4.9 ± 1.3 ferrets km^{-2} from the PIT data and in March at 5.4 ± 2.3 ferrets km^{-2}. In periods S_3 and S_4, the density peaked in March 1997 at 6.3 ± 1.1 ferrets km^{-2} using PITs and 6.2 ± 1.3 ferrets km^{-2} using ear tag data. Ferret density was lowest between October 1996 and January 1997 when no ferrets were captured. The average density of ferrets for the four survival periods from the PIT and ear tag data are shown in Table 2.5. In period S_2, ferret density was lower from the PIT data than the ear tag data but in S_4, ferret density was higher from the PIT data than the ear tag data.

The estimated density of ferrets recruited into the population for the first time between trapping sessions is shown in Figure 2.1d. The pulse of young ferrets recruited into the population peaked in January 1996 at 3.0 ± 1.4 ferrets km^{-2} and in February 1997 at 2.9 ± 1.5 ferrets km^{-2}. Even though ferret recruitment between years was similar, ferret density was higher in 1997 ($t = 3.2$, d.f. = 6, $p = 0.01$) than in 1996. Normally the breeding season for ferrets in New Zealand is between September and March, although few ferrets mate after September and October (Giles and Wallace 1983; Lavers 1973). However, five very young ferrets (from different areas of *Cotswold*) were captured in April and May 1997, possibly indicating that some ferrets bred for a second time that season.

The total number of new captures in periods S_1 and S_2 was 31, and for periods S_3 and S_4 was 53. Thus, the rate of increase between these two years was 58.5%.

2.3.3. Capture probability and survival estimates

Estimated probability of capture, defined as the probability an animal is alive at time *i* is captured in the *i*-th sample, varied significantly between sessions with the lowest period in

Table 2.4. Ferret abundance and density estimates for *Cotswold*.

Period	Trap Nights	New	M	$N_1 \pm SE(\bar{x})$	95% C.I.	Density (km^{-2})	$N_2 \pm SE(\bar{x})$	95% C.I.	Density (km^{-2})
Dec-95	240	3	4	7.5 ± 3.9	-0.3—15.2	1.5	7.5 ± 3.9	-0.3—15.2	1.5
Jan-96	240	2	4	11.7 ± 5.2	3.2—16.8	2.33	11.7 ± 5.2	1.4—21.9	2.33
Feb-96	240	12	17	24.8 ± 6.7	13.8—35.0	4.97	25.8 ± 7.7	10.8—40.8	5.16
Mar-96	240	6	17	20.4 ± 4.2	13.3—29.7	4.07	27.2 ± 11.6	4.5—49.9	5.44
Apr-96	240	1	7	8.7 ± 2.7	3.3—14.1	1.74	6.6 ± 2.6	1.5—11.8	1.32
Jun-96	240	3	7	9.0 ± 2.9	3.2—14.7	1.79	9.3 ± 4.9	0.5—18.2	1.86
Aug-96	240	1	3	10.7 ± 8.7	-6.4—27.7	2.13	10.5 ± 9.5	-8.2—29.2	2.10
Oct-96	240	0	0	0*	0*	0*	0*	0*	0*
Jan-97	360	12	13	29.6 ± 5.8	18.2—41.1	3.98	28.2 ± 7.0	14.4—41.9	3.78
Feb-97	360	13	24	36.4 ± 6.2	24.0—48.7	4.88	33.9 ± 6.5	21.3—46.6	4.55
Mar-97	360	13	25	46.9 ± 8.2	30.7—63.0	6.29	46.7 ± 10.0	26.7—65.9	6.21
Apr-97	320	14	25	36.0 ± 3.2	29.7—42.3	4.83	33.8 ± 4.4	25.1—42.7	4.55
May-97	320	4	18	35.3 ± 5.1	25.3—45.2	4.73	31.1 ± 6.3	18.9—43.4	4.17
Jun-97	320	4	17	39.9 ± 9.7	20.9—58.8	5.35	30.3 ± 11.5	7.8—52.8	4.07
Means		6.28	12.93	24.4 ± 5.6	12.4—32.8	3.73	23.3 ± 7.0	8.9—34.3	3.62

New = New ferrets captured. M = number of marked and unmarked ferrets captured. N_1 = estimated ferret population size using PIT tags. N_2 = estimated ferret population size using ear tags. $SE(\bar{x})$ = standard error of parameter (x) including non-sampling error terms. 95% C.I. = the 95% confidence intervals for N. Density estimates from Dec-95 to Aug-96 are calculated from the trapping grid area for 40 traps plus a distance 0.5 times the mean home range length and the density estimates from Oct-96 to Jul 97 are calculated from the trapping grid area for 60 traps plus a distance 0.5 times the mean home range length. * = value could not be estimated because no animals were captured in the traps set.

Table 2.5. Density estimates (± standard error) of ferrets using either PIT tags or ear tags for the four survival periods.

Period	PITs Density ± S.E (km^{-2})	Ear tags Density ± S.E (km^{-2})
S1	1.91 ± 0.92	1.91 ± 0.92
S2	3.59 ± 0.91	3.97 ± 1.46
S3	2.63 ± 1.03	2.58 ± 1.28
S4	5.21 ± 0.87	4.71 ± 1.03

October and the highest periods in March 1996 and April 1997 (Figure 2.1c). After the pulse of newly recruited ferrets in S_1 and S_3, capture probabilities remained high in S_2 ($\bar{x}$ = 0.74, SE = 0.04) and S_4 ($\bar{x}$ = 0.57, SE = 0.07). The majority of ferrets captured in periods S_2 and S_4 were juveniles and sub-adults (see Chapter 3). After periods S_2 and S_4, the capture probability declined markedly in period S_3 and again started to decline in period S_4.

The longest time a marked ferret was known to reside in the study area was 431 days. This was an adult female. The shortest known time was a ferret which was killed by a farmer on the day following its capture and tagging. Mean known residence from the time of first capture to last recapture was 108 days, SE = 10, n = 98. Not all ferrets were captured in consecutive months as many had a 3-4 month break between recaptures.

From the summary provided by the programme MARK, the best model appears to be model 1 (Table 2.6). The model S(g)p(.)r(.)F(.) = 1 shows that for all but one survival period, S_3, there is a constant probability of capture. It also showed that the tag reporting rate was constant for those periods when tagged ferrets were reported. The S(g) parameter indicates that the survival rate is different between genders. Hence, there is a slight unequal probability of capture between sexes. The longest known residing ferret was a female and the only ferrets captured from one year to the next were also females (n = 4). The F(.) parameter implies that emigration is random, that is, ferrets can leave and come back.

Comparing models 2 and 3 (Table 2.6), provides strong evidence of time variation in survival rate (χ^2 =17.5, d.f. = 3, p = 0.0006). Models 2-6 are explained below:

Model 2. S(g)p(t)r(.) F(.) = 1: As for model 1 but with time-dependent capture probabilities.
Model 3. S(.)p(t)r(.) F(.) = 1: As for model 2 but with survival rate constant across all periods.
Model 4. S(t)p(t)r(.) F(.) = 1: As for model 1 but with no constraints on survival rate.
Model 5. S(t)p(t)r(t) F(.) = 1: No constraints on survival rate, no constraints on reporting rate for those periods with tagged ferrets reported dead by farmers but zero otherwise; random emigration.
Model 6. S(t) p(t) r(t) F(t) = 1: All parameters unconstrained; permanent emigration.

The parameter estimates for model 1 (S(g)p(.)r(.)F(.) = 1) are given in Table 2.7. Two main observations can be made about the model and its parameters. First, multiplying all survival periods together produced an erroneous result as the standard error for the first

Table 2.6. Model fitting summary for programme MARK™.
Models include time (t), gender (g) and exclusion of these parameters = (.).

Model	Movement (emigration)	AIC_c	ΔAIC_c	No. parameters	Deviance
(1) S(g)p(.)r(.)F(.) =1	random	592.352	0.00	6	290.365
(2) S(g)p(t)r(.) F(.) =1	random	600.654	8.302	20	266.432
(3) S(.)p(t)r(.) F(.) =1	random	610.835	10.18	17	283.936
(4) S(t)p(t)r(.) F(.) =1	random	623.355	12.52	32	257.229
(5) S(t)p(t)r(t) F(.) =1	random	640.349	16.99	38	256.498
(6) S(t) p(t) r(t) F(t)		678.648	38.29	53	244.155

NOTE: The fullest model includes movement parameters under the assumption that emigration is permanent (F_i is the probability a ferret remains in the study area). The random emigration model assumes that the probability an animal is available for recapture does not depend on whether it was available for capture the previous trapping period.

Table 2.7. Parameter estimates under model S(*g*)p(.)r(.)F(.)=1. Parameters: $S_{1\text{-}4}$ = the four survival periods 1, p = probability of capture and r = the probability that a ferret that dies between trapping periods, is killed by a farmer and its tag reported.

			95% CI	
Parameter	Estimate	SE	lower	upper
S_1	1.000	0.000	1.000	1.000
S_2	0.650	0.061	0.524	0.758
S_3	0.921	0.045	0.778	0.975
S_4	0.860	0.040	0.761	0.922
p	0.474	0.038	0.401	0.548
r	0.582	0.093	0.398	0.746

survival rate was not valid (Table 2.7). The problem is that the estimate is right on the boundary of the parameter space and currently no valid estimate can be derived in MARK.

Nevertheless, the survival rate of tagged ferrets from the model was 51% per annum. Unfortunately, because data were not separated into different sexes, gender survival rates cannot be reported. Nevertheless, it is possible that some disparity between sexes may have been present based on trap-catch rates (see Chapter 3).

Second, trapping by farmers in and around the study site affected ferret survival. This is evident in periods S_2 and S_4 where the estimated survival rate is lower than in periods S_1 and S_3 when farmers were not trapping (Table 2.1). The estimated probability of survival between trapping sessions is shown in Figure 2.1. Here, ferret survival declined in periods S_2 and S_4 after an initial pulse of newly captured ferrets. Ferret survival may have been much higher had the farmers not trapped during these periods. The number of ferrets trapped by farmers in periods S_2 and S_4 are shown in Table 2.3.

2.4. Discussion

2.4.1. Tag evaluation

Ferret population estimates were more precise and less biased using PITs compared to ear tags. Although only six percent of the population would have been unidentifiable with the PIT system, the population estimates were only marginally different. Nevertheless, two integral assumptions of any CR study are, firstly, that animals do not lose their tags and, secondly, that all tags be recorded accurately (Manly 1971). Using only ear tags in this study would have violated both of these assumptions. Tag loss, of this degree, could have spoiled data on movement or dispersion studies, as well as tests on equal catchability (Arnason and Mills 1981).

Although the Jolly-Seber estimates for the two tagging systems did not differ markedly, the time it took to identify and accurately record a recaptured ferret did differ. Reading the ear tags of a ferret took longer and could, on occasion, be quite troublesome. Even though feral ferrets can be quite docile (Lavers and Clapperton 1990), they still had to be handled so the ear tags could be read. In many instances the ear tags were marked or covered in dirt, making them difficult to read. In contrast, PITs could be read without having to handle or place the ferrets into the crush bag. In some PIT studies, human contact

has been eliminated altogether by placing scanning antennae along runways and in resting boxes (Becker and Wendeln 1997; Harper and Batzli 1996). Scanning ferrets for their ID code without having to handle them, as well as the short time it took to identify the ferrets accurately, are seen as a major advantages over ear tags.

The main disadvantage of PITs is that they are much more expensive than ear tags. PITs cost between NZD $12—$15 per tag and NZD $700+ for the MPR scanner whereas ear tags cost NZD $0.44 per tag or $0.88 per ferret (plus applicator pliers which cost NZD $54; Chemstock Animal Health, Ltd., N.Z). In my experience, ear tag loss, resulting in biased survival and recruitment estimates, superseded the higher cost of the PIT system. However, if only abundance estimates are required, a small number of tags losses may not bias estimates significantly; therefore, the decision whether to use PITs or ear tags in a CR study depends upon the purpose for which the estimates are required (Arnason and Mills 1981).

Two other minor considerations should be mentioned about PIT tagging systems. Firstly, the size of the portable scanners. Although the MPR used in this study was compact and had a lightweight design, its dimensions were 306 mm L x 126 mm W x 50 mm H and its weight was 700 g. However, smaller pocket scanners only 170 mm L x 80 mm W x 32mm and weighing 308 g are now available (Destron-Fearing Corp., St. Paul, USA). Second, as with most portable electronic equipment, MPR scanners are liable to battery failure; therefore, a second set of batteries should always be carried. These should not necessarily be seen as disadvantages; however, it must be noted that, compared to ear tagging, with PIT tagging systems more can go wrong in the field.

Double tagging with two ear tags is possibly one way to increase the likelihood of identifying an animal (Seber and Felton 1981). Certainly, ferrets in a 2 year home range study in New Zealand that were tagged in both ears had a lower tag loss rate (3.2%) than in my study (Norbury *pers comm.*). However, double tagging does not solve the problem when ear tags, which are secured to the outside of an animal, inevitably fall off. This occurs either because they accidentally fall off (e.g. Weddel seals), or are deliberately torn off, as occasionally happens when sheep push or rub their heads against fences (Hunt 1994; Testa and Rothery 1992). Polecats and ferrets spend much of their time underground and moving through the vegetation under-canopy (Blandford 1987). They also groom themselves with their large claws. It is possible that some ferrets, when grooming or moving around, may accidentally catch their ear tags and pull them off. Ear tags may also

fall off if they are tightened too tightly on the ear pinnae, consequently the ear rots and the tags fall off easily.

Female ferrets appear to lose their ear tags more frequently than males. Ferrets are sexually dimorphic, with male ferrets being almost twice the size of females (Dayan and Simberloff 1994); therefore, males may be less inconvenienced by the weight and size of the ear tags. However, for female ferrets, who have proportionately smaller ears, ear tags may be a bigger nuisance. In addition, mating behaviour in ferrets is extremely vigorous and prolonged, with males biting the back of the neck and head of the females and dragging them around (Poole 1972). During this courting and mating period, it is possible that female ferrets may lose ear tags. Male ferrets may lose their ear tags in encounters with other males in their territory as they are prone to biting each other around the neck and ear region (Poole 1973). Understandably, ear tags may be ripped off during this aggressive behaviour.

Tests for any detrimental effects of PITs on snakes, cats, dogs, and birds have so far shown them to be safe and reliable (Carver *et al.*, 1999; Keck 1994; Sorensen *et al.*, 1995). However, PITs can be lost through migration out of the implantation site (Freeland and Fry 1995; Germano and Williams 1993; Hunt 1994); nevertheless, this problem has been solved by applying a biologically safe adhesive to close the puncture wound (Seebeck and Booth 1996).

As PIT tagging systems are utilised more, the price of PITs will undoubtedly drop and scanning ranges will increase with advances in technology. But until then, the small loss in precision and accuracy using double ear tagging may be acceptable especially if only abundance estimates are required. Nevertheless, if high precision is required then using a PIT tagging system would be a preferable option.

2.4.2. Ferret abundance and survival

Estimated ferret abundance generally followed a marked seasonal pattern. That is, young ferrets were recruited into the population from December to January and the population remained high until June and July after which the population declined until the beginning of a new recruiting season. This pattern is similar to other ferret populations studied in New Zealand (Lavers 1973; Norbury and Heyward 1997; Ragg 1997). One notable exception to this commonly observed seasonal pattern was when several very young ferrets

were trapped in April and May 1997. A similar pattern from a ferret population only ten kilometres away was also reported during May 1997 (Caley *et al.*, 1998).

Herter (1953) reported that juvenile polecats in Europe achieve independence from their mothers at two to three months old. Because ferret behaviour is similar to that of polecats (Blandford 1987), it can be assumed that juvenile dispersal would have been in late December and January for kittens born in October (Caley *et al.*, 1998). Given that the gestation period for ferrets is 42 days (Giles and Wallace 1983), it is possible that a second litter of ferrets could have been born in February and March. Hence, the young ferrets captured in April and May 1997 in both studies could have been a second litter of ferrets dispersing from their natal areas. Unfortunately, it is not known if the young captured were from females that had bred earlier that season. Nevertheless, the dual timing of young captured on both my study site and that of the site ten kilometres away would suggest that either some females did breed twice that year, and/or the recently born ferrets seen in April and May 1997 were produced by sub-adult ferrets that had been born in October 1996. However, it is unlikely that early breeding sub-adults were responsible for the second litters of young found on both sites as, with polecats (Walton 1977), ferrets begin to breed only in the year following their birth. Certainly, climatic conditions and prey availability would have been favourable for the ferrets, as lagomorph numbers, their primary prey, had increased dramatically after October 1996 (Caley *et al.*, 1998; see Chapter 1).

It is well documented that primary prey abundance often affects predator abundance (Pech *et al.*, 1992; Sinclair and Pech 1996). Ferrets generally produce between two to ten kittens in a litter; however, many die before reaching a trappable age (Ragg 1997). If kitten survival improved as a result of increased prey availability, and if double breeding did in fact occur, then a subsequent numerical increase of ferrets would be observed. Indeed, this is evident from a trapping study subsequently carried out on *Cotswold* the following year where the number of new ferrets captured in 1998 was 111 (Schabort *pers. comm.*), doubled the number captured in 1997. Previously, only 31 new ferrets had been trapped in 1996 and 53 new ferrets in 1997. Although ferret numbers increased, their rate of increase was approximately the same between each year. This rate of increase coincided with the increase in lagomorphs (see Chapter 4).

Recruitment of young ferrets in January and February is probably the most influential factor in the seasonal pattern of ferret numbers. Capture probabilities during summer and autumn remained high after the influx of new ferrets, most probably because

they would encounter many traps in their search for a territory and they were inexperienced in avoiding them. This was also seen in two separate sites in North Canterbury, where 90% of all ferrets trapped over the summer and autumn period were juvenile or sub-adults (Caley *et al.,* 1998). Recapture probabilities remained high until mid-winter, but fell markedly in late winter and in spring. This decline is significant as it suggests that trapping ferrets, especially during the breeding season, may be extremely difficult. Thus, the low probability of capturing adult ferrets has major implications on the timing and effort required in future ferret control programmes.

Ferret density estimates in this study ($\approx 5km^2$) were similar to those found on three different farms in the semi-arid lands of central Otago where ferret density varied between 2-5 ferrets km^{-2} (Norbury and Heyward 1997). Similarly, Middlemass (1995) reported a mean density of 4.4 ferrets km^{-2} at Macraes Flat in Otago, and Ragg (1997) reported a mean density of 4.6 ferrets km^{-2} on farmland near Palmerston also in Otago. Ragg (1997) thought her study site supported an unusually high abundance of ferrets, though my results suggest this may not be the case.

Only four ferrets captured in 1996 where recaptured in 1997. All four were females. However, 14 ferrets (9 ♀: 5 ♂) tagged in 1996/97 were recaptured in 1998 (Schabort *pers. comm.*) Although the longest time a marked ferret was known to reside in my study was 431 days, Schabort (*pers. comm.*) who used the same study site in the following year, reported capturing a female in 1998 that had been tagged in 1996. Thus, the longest known residing ferret was 704 days ($\approx$ 23 months). It was estimated that this ferret, which was considered to be an adult when first captured, would have been at least 3-3.5 years old. Other studies support this finding; at Pukepuke Lagoon male ferrets were found to reside, on average, between 7.8-9.9 months, while females resided on average between 14.6-20.3 months (Moors and Lavers 1981).

In this study, annual ferret survival was 51%. Similar, annual survival rates of 47% and 54% were also reported for radio-collared ferrets on one farm in Central Otago and another farm in the MacKenzie Basin (Norbury and Heyward 1997). This is high compared to polecats in Europe (Blandford 1987); however, ferrets in New Zealand do not suffer from as many parasites and diseases, and have virtually no natural predators (Lavers and Clapperton 1990). Differential survival rates between sexes could not be analysed in this study, as the data were pooled; however, female ferrets appear to survive longer than males.

Recaptures were not always in consecutive trapping sessions as some ferrets recorded large (3-6 month) gaps between recaptures. Large recapture gaps appear to be a feature of ferret trapping programmes as both Ragg (1997) and Lavers (1973) also found this pattern. Generally the largest gaps in recapture occurred from August to January; therefore, few ferrets were captured during winter and spring. However, fewer trapping sessions occurred between these months. During Spring 1995 only four (2♀, 2♂) ferrets were captured for the first time, while in the winter/spring of 1996 only one new ferret (♂) was captured. Additionally, only two ferrets (2♂) were captured in December 1996 by the farmer using 21 leg-hold traps over seven nights (D. McLean *pers comm.*).

Low catch rates during winter and spring are not unusual and several hypotheses have been proposed to explain this phenomenon. Winter and spring coincides with the main breeding season for lagomorphs, the primary prey of ferrets, and with an excess of prey available, ferrets may avoid baited traps (Norbury and Heyward 1996). Late winter and spring is also the main breeding season for ferrets and, therefore, it is understandable that fewer female ferrets were captured during winter and spring than at any other time of year. Ragg (1997) found a strong sex bias in trap catch rates during the breeding season; females were seven times less likely to be caught than males. Thus, the low trappability rate may be a behavioural function of ferrets. Some factors, such as avoiding traps or simply not encountering them, may also affect trapping. Other factors affecting trap success are discussed in Chapter 3.

Alternatively, if ferrets show little neophobia to traps and there are at least 1 or 2 traps in their home range, the low capture-rates during the winter/spring period may be a function of ferret density. Juvenile polecats have a high mortality rate in their first year of life with a life expectancy from birth of only 8.1 months (Blandford 1987). Assuming the same is true for ferrets in New Zealand, ferret abundance would be lower in winter and spring than in summer and autumn. Indeed abundance was at its lowest in winter and spring in this study. Thus, the low trap catch rates observed for ferrets in winter and spring is a combination of both reduced abundance as well as reduced trappability.

However, confounding the low trap catch rate in the summer and autumn before winter and spring was the fact that 11 tagged ferrets (representing 38% of the tagged ferrets on *Cotswold*) and 18 untagged ferrets were killed by neighbouring farmers in summer and autumn, i.e., after the breeding season. This added mortality factor would have contributed to the low abundance estimates recorded in winter and spring.

No ferrets were trapped and killed by farmers on the boundary of *Cotswold* in the two years preceding 1996 (D. McLean *pers. comm.*) and the ferret population during this period was considered to be quite low (Peter Reid, *pers. comm.*). Ferret numbers on a nearby farm (Tiromoana) were also low in 1995 compared to the following years (Caley *et al.,* 1998). Lagomorph numbers were relatively stable and at low levels from 1975 to September 1996 (Bell 1990; Caley *et al.,* 1998); presumably the ferret population was also low. From April 1986 to July 1988 on a farm which is less than 1 km away, 65 ferrets were caught (Robson 1993). The number of ferrets captured in Robson's study is similar to the low number of ferrets caught in the first year of my study. It was only after lagomorph numbers increased dramatically that ferret numbers doubled from one year to the next.

Schabort's data supplement mine to suggest that numerically more young ferrets were recruited into the population in the 1997/98 season compared to the 1995/96 season. On the other hand, ferret survival may have higher in the 1996/1997 season but ferrets were trapped and killed by farmers. Certainly ferret survival did decline in periods S_2 and S_4 when the farmers were trapping, but it is uncertain whether this was also due to natural mortality.

It should be noted that in the months when only a few ferrets were captured, the JOLLY variance population estimates appear more accurate than they really are and it is possible the population size is overestimated. In addition, because the data in this study were pooled, variation in capture probabilities may be masked by heterogeneity in the data. Heterogeneity can vary from one individual to another and may result in negatively-biased abundance estimates (Carothers 1979; Nichols and Pollock 1983). Therefore, the effect of heterogeneity (i.e., differences in age, sex and trap response) is to underestimate population size (Otis *et al.,* 1978).

In summary, ferret abundance followed a marked seasonal pattern. Ferret numbers were high after recruitment in the summer and autumn period and, apparently, very low in the winter and spring period. The decline in ferret abundance and capture probabilities over winter and spring has major implications for ferret control programmes, especially those that want to target females during the breeding season. The low capture rate in the winter and spring period was considered to be a combination of reduced abundance as well as reduced trappability. Ferret density in my study area of North Canterbury (2-5 ferrets km^{-2}) was similar to that found for most other New Zealand ferret studies, and annual ferret survival was 51%.

In conclusion, capture-recapture models used to estimate abundance and survival rely on several assumptions. One of the most crucial, though often overlooked, is that animals do not lose their identification marks and that all marks are recorded accurately (Manly 1971; Begon 1979). Ear tag loss means that the estimates produced in the Jolly-Seber model could be biased; however, with only 6% of the population possibly unidentified over 22 months, the loss in precision of abundance caused by ear tag losses was negligible. Nevertheless, a PIT tagging system is recommended if a more precise and long-term estimate of survival and recruitment is required.

Chapter Three

Relating trapping success to ferret habitat use and movements in North Canterbury, New Zealand.

3. Abstract

Trapping is the most common ferret (*Mustela furo*) control technique used in New Zealand; however, poorly designed trapping programmes are likely to waste money and resources. Future ferret control programmes, especially those aimed to prevent the spread of bovine tuberculosis (*Mycobacterium bovis*), would benefit from understanding key factors that affect ferret trapping success. In this study, traps were set using a systematic sampling method throughout a 500 ha area of North Canterbury farmland. Data gathered on key habitat features as well as predator-prey distribution were modelled using GLIM, Mantel randomisation tests, and GIS techniques. No significant differences in trapping rates between sexes were detected and, as a result, all data were pooled. The main factors found to influence trap success were the presence of vegetation cover, rabbit sign and animal tracks. However, other factors, such as the number of non-target species in an area, excess prey availability, and individual differences in trapping behaviour may have influenced trap success. Additionally, results showed that male ferrets generally travel greater distances than females, roaming over larger areas of land. However, compared to Year One, defended territorial areas using the minimum convex polygon method, declined for both sexes during Year Two and, as a consequence, the trapping data displayed two distinct spatial patches where ferrets were mainly caught. One factor affecting this decline could have been the corresponding increase in lagomorph numbers. In analysing site fidelity and homing ability, it was found that female ferrets exhibited stronger territoriality than males, and were more often recaptured near their original capture site. Consequently, information about ferret movements and habitat use would greatly assist trap placement planning in Tb management programmes.

3.1. Introduction

Generally, animals are not randomly dispersed throughout a habitat. The most common spatial pattern is an aggregated distribution where animals live, or are forced to live in close proximity (Perry 1995). Animals select habitats based on both environmental and intrinsic factors (Krebs 1994). Environmental factors may include rainfall, temperature or habitat type, and intrinsic factors may include density dependence, food exploitation or social behaviour. Most mammals have an area of ground which they frequently patrol and are well acquainted with (Riney 1982). This is defined as their home range.

A territory is a fixed space from which an individual actively excludes competitors of their own species from a specific resource or resources (Maher and Lott 1995). With intrasexual territoriality, individuals exclude only members of the same sex and tolerate members of the opposite sex (Powell 1994). Intrasexual territoriality has been observed in several mustelid species, including polecats (*Mustela putorius*: Lodé 1996a), which are the ancestors of feral ferrets (Heptner 1964). Powell (1993) predicted that, as prey densities change from low to high, sexually dimorphic mustelids like ferrets should change from having intrasexual territories to having home ranges that overlap extensively with members of both sexes.

Because males compete for access to breeding females, they generally have larger home range areas during the breeding season than females, who require only a small area around the time of parturition. Home range size, and thus habitat use, is a dynamic process that can change according to prey abundance, habitat quality, breeding or non-breeding season, as well as the age, sex and health of an animal, and an animal's relationship with conspecifics (Herrmann 1994). Hence, habitat use and home range size are the result of the behaviour adopted by an animal to survive and maximise its reproductive success (Sandell 1989b).

Although there have been various studies on ferret home range length and size in New Zealand (Lavers 1973; Moors and Lavers 1981; Ragg 1997; Norbury *et al.*, 1998b), behaviour associated with trapping has rarely been discussed. Site fidelity and homing ability have not been studied in ferrets. Site fidelity is important because, if an animal is familiar with an area, it will be able to learn the locations of food resources, den sites, escape routes and it will have repeated contacts with conspecifics (Munger 1984). Homing ability is important in saving time and energy when animals are out hunting for prey

(McFarland 1981). These movement parameters are also important for addressing questions on repopulation rates after predator control operations.

Trapping can be a powerful tool in monitoring and controlling predators if the programmes are well designed and implemented correctly (Brown and Miller 1998). Questions such as those associated with age structure, sex ratio, population abundance and distribution can be answered using trapping techniques (Caughley 1977; Krebs 1994). Trapping has also been useful in New Zealand to investigate whether ferrets (*Mustela furo*) transmit bovine tuberculosis (*Mycobacterium bovis,* Tb) to livestock (Caley *et al.,* 1998), and for monitoring and controlling predators living near threatened wildlife populations (King *et al.,* 1996a; McLennan *et al.,* 1996).

Targeting a specific species in a trapping programme is not always straightforward. Many factors can influence trap success, such as, trap location (Caley 1994; Lodé 1994), trap spacing (to avoid capturing one sex more than the other: King 1975; Buskirk and Lindstedt 1989) effectiveness of lures and baits (Clapperton *et al.,* 1994; Dilks *et al.,* 1996); and the number of non-target species present. The relative importance of these factors depend upon the aim of the trapping programme; i.e., whether the objective is to control the predator population or just to sample it (King 1994).

In addition to these factors, many life history traits of the target animal need to be considered. Most small carnivores are solitary, never co-operating with conspecifics to rear young, forage together or to defend resources against predators (MacDonald 1983). The main reason for this solitary existence probably relates to the prey characteristics and the hunting mode of the predator (Sandell 1989b). Therefore, to trap ferrets which are solitary animals that primarily hunt lagomorphs (rabbits; *Oryctolagus cuniculus* and hares; *Lepus europaeus*: Walton, 1977), trap placement should allow for not only the hunting mode of ferrets, but also the prey characteristics, particularly those of lagomorphs.

Trapping ferrets to remove them in control operations is common practice in New Zealand (Cross *et al.,* 1998). Poorly designed trapping programmes, where traps are set out in areas unlikely to catch ferrets, will waste resources. This chapter presents data on ferret movements in relation to habitat selection and other biological factors, such as non-target species, that are likely to influence trapping success.

3.2. Methods

3.2.1. Study areas

Two farms 80 km north of Christchurch, New Zealand (43°02'S., 172°59'E), were selected because of their similar topography, vegetation, and climate. The first farm, *Cotswold*, consisting of a 507 ha core area, was bordered by a 500 m buffer zone to the north and west. *Cotswold* was designated a non-treatment site to monitor natural fluctuations in ferrets and prey (lagomorphs) abundance. Because ferrets were not removed from this site the buffer zone allowed for neighbouring farmers who were concerned about releasing ferrets that could potentially spread Tb. The second farm, *The Rock*, consisting of a 453 ha area with no buffer zone, was used as a treatment site. In contrast to *Cotswold*, all predators were removed as part of a study investigating the effect of experimentally controlling predators on the rate of increase of lagomorphs. Only one farm separated the two study sites; this was approximately 1 km wide. For further details of the study sites see Chapter 1.

3.2.2. Ferret trapping

Trapping sessions were carried out over two years. Year One included trapping during October and December of 1995, January to April, June, and August of 1996. Year Two including trapping during October 1996 and January to July of 1997. During a trapping session, each trap was set for six consecutive nights and checked daily. For the first six months on each site, until April of 1996, predators were caught using wire cage traps; 40 on *Cotswold* and 40 on *The Rock*. The captured ferrets were tagged and released as part of a concurrent capture-recapture study (see Chapter 2). After April 1996, all predators caught on *The Rock* were removed while on *Cotswold*, the capture-recapture study continued. In October 1996 and from January to February of 1997, an extra 20 cage traps were used on *Cotswold* in an additional 100 ha.

Because of farm management constraints, accidentally catching predatory birds (e.g., Australasian Harriers; *Circus approximans*) and the topography of the farms, traps were not evenly distributed throughout the properties. Mean inter-trap distance was 237 m (range: 100—500 m). Although the traps were set at varying distances, two considerations were made for their placement. First, they were set to allow an even representation of all

possible trapping variables (see below) and second, once a representative area was chosen, the traps were set in situations most likely to catch ferrets. A global positioning satellite (GPS) recorder was used to estimate each trap location and this data was entered into the geographic information system (GIS) programme, ArcView®.

Traps were baited with skinned rabbit meat. Bait was replaced daily in the summer and every second day in winter. All ferrets captured in the first six months were sexed, aged, tagged and then released. A new ferret was defined as an unmarked ferret that had never been captured before. A recaptured ferret refers to a previously marked ferret. In all analyses, recapture results do not include the original capture occasion.

If a ferret was captured in only one trapping session it was defined as either a transient which was a neighbouring ferret, or a resident that had died before the next trapping session. If a ferret was captured on more than three occasions, over three trapping sessions or more, it was defined as a resident (Moors and Lavers 1981). Juveniles were classified as ferrets < 3 months old (caught mainly between October and January) and sub-adults as 3-8 months old (caught between February and August). Occasionally it was difficult to discriminate between sub-adult and adult ferrets, but if a large sagittal crest was present and females showed signs of lactation or males showed signs of fighting scars, they were considered adults. No sub-adult ferrets were found after August; hence, sub-adult ferrets were trapped only from January through to August.

Straight-line distance measurements travelled by the ferrets caught on consecutive nights were calculated in ArcView®. All sprung traps and non-target species caught were also recorded.

3.2.3. Trap success

To standardise trap-catch indices between years, only ferrets caught in the original 40 traps on the first five nights were analysed. Trap success (Nelson and Clark 1973) was calculated as:

$$\text{Corrected trap nights (CTN)} = \frac{\text{the number of ferrets caught}}{\text{ATN}} \times 100$$

$$\left(\text{ATN} = \frac{\text{non-target species + sprung traps}}{2} - \text{number of traps set per night}\right)$$

Even though trap success is corrected for the number non-target species trapped, each non-target species caught reduces the potential for capturing a ferret. Mann-Whitney tests were used to test whether non-target species trapped on *The Rock* were the same as on *Cotswold.*

a) ***Factors that influenced trap success***

To analyse which factors influenced trapping success, the total number of ferrets captured per trap were fitted to a generalised linear model using the programme GLIM (Anon 1987). The model was fitted with a log link function with a Poisson error structure and refitted with a correction for overdispersion (the deviance was rescaled to the ratio of the deviance divided by the model degrees of freedom). At each trap site all variables were categorised into 2 factors using a presence/absence technique. The full model (i.e. all the factors included, though no interactions) was fitted first and a deletion test was carried out by removing each variable in turn and assessing its contribution to the overall model deviance. The least significant variable was then removed and the process repeated until the model contained only significant terms (at the 0-10 level). The ratio of each parameter to its standard error was used to calculate the *t*-statistic (Crawley 1993).

The factors represented in the model were: (1) presence of water (< 20 m); (2) whether the trap was set near cover (< 0.5 m); (3) type of cover 1: long grass or scrub; (4) type of cover 2: native bush and trees; (5) whether the pasture was grazed (below 5 cm in height = grazed); (6) presence of lagomorph sign (rabbit burrows, breeding stops and/or rabbit latrines) within a 10 m radius; (7) whether the trap was set near (< 5 m) the boundary of a gully and pasture; (8) whether the trap was set along an animal path or track (animal paths may be created by farm livestock or by feral animals), (9) whether the trap was set next to a fence or in a human structure such as a barn, and (10) whether the trap was set on a slope or flat land.

The weather was assigned to one of three classes at 2300 hours on each night of trapping: fine (no or few clouds), wet (raining: snowfall was also classified as wet weather) or cloudy (no rain, but cloud reduced the moonlight). The effect of weather on trap success was investigated using a chi-square analysis for each class of weather based on the trap-catch per 100 CTN.

b) ***Relationship between trap location and trap-catch***

The relationship between the inter-trap distances and the differences between trap-catch success at individual trap locations was examined using a Mantel randomisation test

(Manly 1997). This test measures the association between the elements in two matrices by correlation and determines the significance of this comparison with the distribution found by randomly reallocating the order of the elements in one of the matrices. One thousand simulations were performed on the data. The first matrix was the distances between traps and the second matrix was the differences in the number of ferrets caught in each trap. If there was spatial aggregation (high correlation between trap distances and count differences) then traps located close together would have similar counts.

3.2.4. Movement of ferrets

Only 11 ferrets were live captured on *The Rock* from October 1995 to April 1996. Because all ferrets caught after April 1996 were removed, the results on the distribution and site fidelity of ferrets refers to animals captured or released on *Cotswold* only.

To construct a 100% minimum convex polygon (MCP: (Mohr and Stumpf 1966) only resident sub-adult or adult ferrets, captured in at least three different traps over three separate sessions or more, were used. Variability in trap response of individual ferrets within trapping sessions, and between trapping sessions, meant that the MCP areas drawn are not representative of ferret home ranges. Instead they represent minimum movement areas only. Consequently, the MCP areas are used only as an aid to delineate a ferret's movements and distribution (where a ferret has moved and was trapped) and not its supposed home range.

To compare MCP areas between years, only data from the non-breeding season (January-June 1996 and January-June 1997) was used. This was done for two reasons: trapping and recapture rates were at their highest at this time of year and the spatial distribution of captures would not be influenced by mating behaviour. However, it is acknowledged that the spatial distribution and movement of ferrets may change considerably during the breeding season.

Most movement data is descriptive; however, two-way analysis of variance was used to test the null hypothesis that the movement distances and MCP areas of ferrets did not differ between sexes and ages. Since MCP areas and movement distances were skewed to the right, the data were transformed using $\log_{10}$. All MCP area calculations were performed using the *Animal Movements Analysis* extension in ArcView® (Hooge 1998). To estimate the proportion of ferret MCP areas that overlapped, each individual ferret's MCP

area was overlaid on top of graph paper and compared with the MCP area of every other ferret. The percentage area obtained from this was then averaged for each year to calculate a within and between sexes proportion.

3.2.5. Site fidelity and homing ability

To test whether ferrets restrict their movements to territorial areas or roam at random, a site fidelity test was performed in ArcView®. The site fidelity function is a variant of the method described by Spencer *et al.* (1990), and uses a Monte-Carlo simulation and parameters from the point data set of each ferret to determine if the observed movement pattern has more site fidelity than should occur randomly. To compare the observed movement pattern of a ferret, 1000 iterations based on a ferret's trap history were used to extrapolate the actual movement path of each ferret (Hooge 1998). The actual movement path was based on where the ferret was first captured and the location of all sequential captures thereafter. In addition to the site fidelity test, 14 ferrets (7 females and 7 males) from *The Rock* were translocated to *Cotswold* and released at different times and in various locations to determine where they would next be captured.

3.3. Results

3.3.1. Trap Results

Capture data for the ferrets are summarised in Table 3.1. In total, 84 new ferrets on *Cotswold* and 59 new ferrets on *The Rock* were captured. The mean number of times an individual ferret was captured on *Cotswold* was 6.7 (SE = 0.71; range 1-16). The mean number of times an individual ferret was recaptured on *The Rock* was not calculated because most ferrets captured were killed.

The number of individual ferrets captured in each trap ranged from 0-5 (Figure 3.1a) and the total number of captures in each trap ranged from 0-20 (Figure 3.1b), while the proportion of individual ferrets caught in each trap is shown in Figure 3.1c. However, these graphs do not show the differences in catch rates between years. In Year Two, 11 of the 20 additional traps never captured any new ferrets and 7 of these never caught any ferrets at all. However, one new trap (47) captured more ferrets than any other trap but only 10% of these captures were new ferrets.

Table 3.1. Number of ferrets caught from October 1995 to July 1997 on *Cotswold* in 4014 available trap nights and on *The Rock* in 3677 trap nights. (N = no. of new captures and R = no. of recaptures [excluding original capture]).

		Cotswold		*The Rock*	
		N	R	N	R
Male					
	Adult	22	68	19	10
	Sub-adult	24	62	14	11
	Juvenile	3	3	0	0
	Percent of males captured	58	60	52	51
Female					
	Adult	18	63	22	10
	Sub-adult	15	24	8	10
	Juvenile	2	3	0	0
	Percent of females captured	42	40	48	49

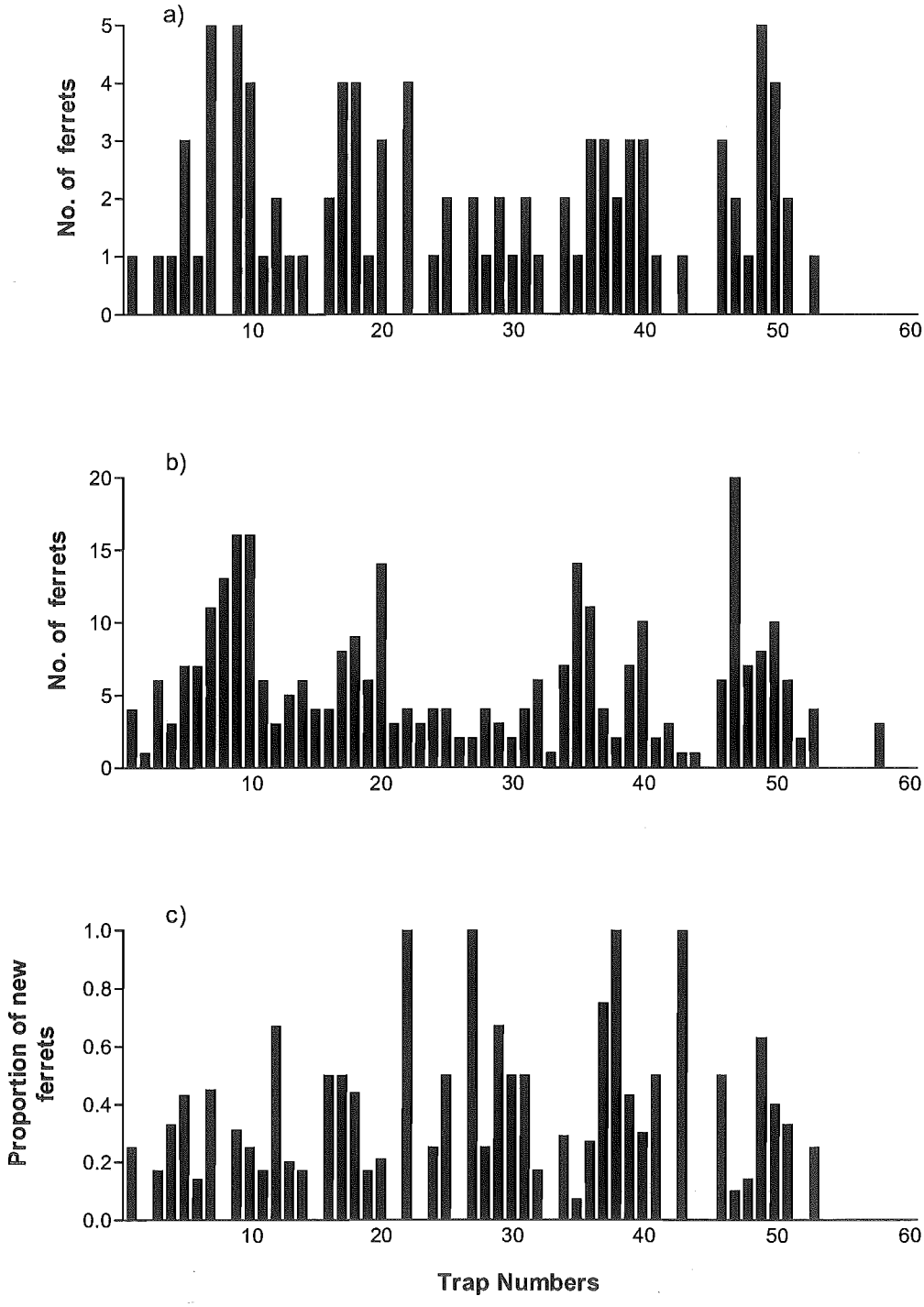


Figure 3.1. Number of ferrets caught in each trap. Traps 1-40 were operational from October 1995 to July 1997. Traps 41-60 were operational only from October 1996 to July 1997. (a = new ferrets caught in each trap, b = all ferrets caught, c = proportion of new ferrets caught [new ferrets/all ferrets]).

Male ferrets made up 58% of all new captures and 60% of all recaptures on *Cotswold* (Table 3.1). The sex ratio of both new and recaptured ferrets on *The Rock* was close to unity (Table 3.1). More new ferrets were captured on *Cotswold* in Year Two (21 females: 32 males) than in Year One (14 females: 17 males). Similarly, on *The Rock* more new ferrets were captured in Year Two (23 females: 27 males) than in Year One (7 females: 6 males). Adult female and male ferrets were equally likely to be recaptured but sub-adult males were more likely to be recaptured than sub-adult females (Table 3.1).

Trap success for both properties varied seasonally with more ferrets captured during summer and autumn than in winter and spring (Figure 3.2). The number of new ferrets caught peaked at 6.6 per 100 corrected trap nights (CTN) in February 1996 on *Cotswold* and at 8.3 per 100 CTN in April 1997 on *The Rock*. For all ferrets (new ferrets + recaptured ferrets), the trap-catch rate peaked at 17.7 per 100 CTN on *Cotswold* and 10.5 per 100 CTN on *The Rock* (during the first six months when ferrets were being released). The recapture rate on *The Rock* during April to July 1997 was for ferrets translocated to *Cotswold* and later recaptured on *The Rock* (see below). The lowest trap-catch rate was from August to December when only a few ferrets were caught.

The number of non-target species captured on both properties is given in Table 3.2. In Year One, the number of non-target species trapped on *The Rock* was more than double that trapped on *Cotswold,* but in Year Two the number of non-target species trapped was the same. Hedgehogs (*Erinaceus europaeus*) were the most common non-target species trapped, followed by possums (*Trichosurus vulpecula*) on *The Rock*. Hedgehogs were also the most common non-target species trapped on *Cotswold*. However, numerically more hedgehogs were trapped in Year Two on *Cotswold* and fewer were captured on *The Rock* (Table 3.2). However, neither of these changes were significant: (*The Rock*: $U = 4.5, p = 0.09$; *Cotswold*: $U = 11, p = 0.75$).

Rats (*Rattus rattus* and *R. norvegicus*) and stoats (*Mustela erminea*) were the only non-target species that increased significantly between years on *The Rock* (where ferrets and cats, *Felis catus,* were being removed in Year Two: Table 3.2). Rats increased from a mean of 0 per trapping session in Year One to 0.92 per trapping session in Year Two ($U = 2.5, p = 0.018$), and stoats increased from 0 per trapping session in Year One to 0.32 per trapping session in Year Two ($U = 2.5, p = 0.018$). Correspondingly, rat ($U = 7, p = 0.21$) and stoat ($U = 12.5, p = 1$) numbers did not change significantly on *Cotswold* (where no ferrets or cats were being removed).

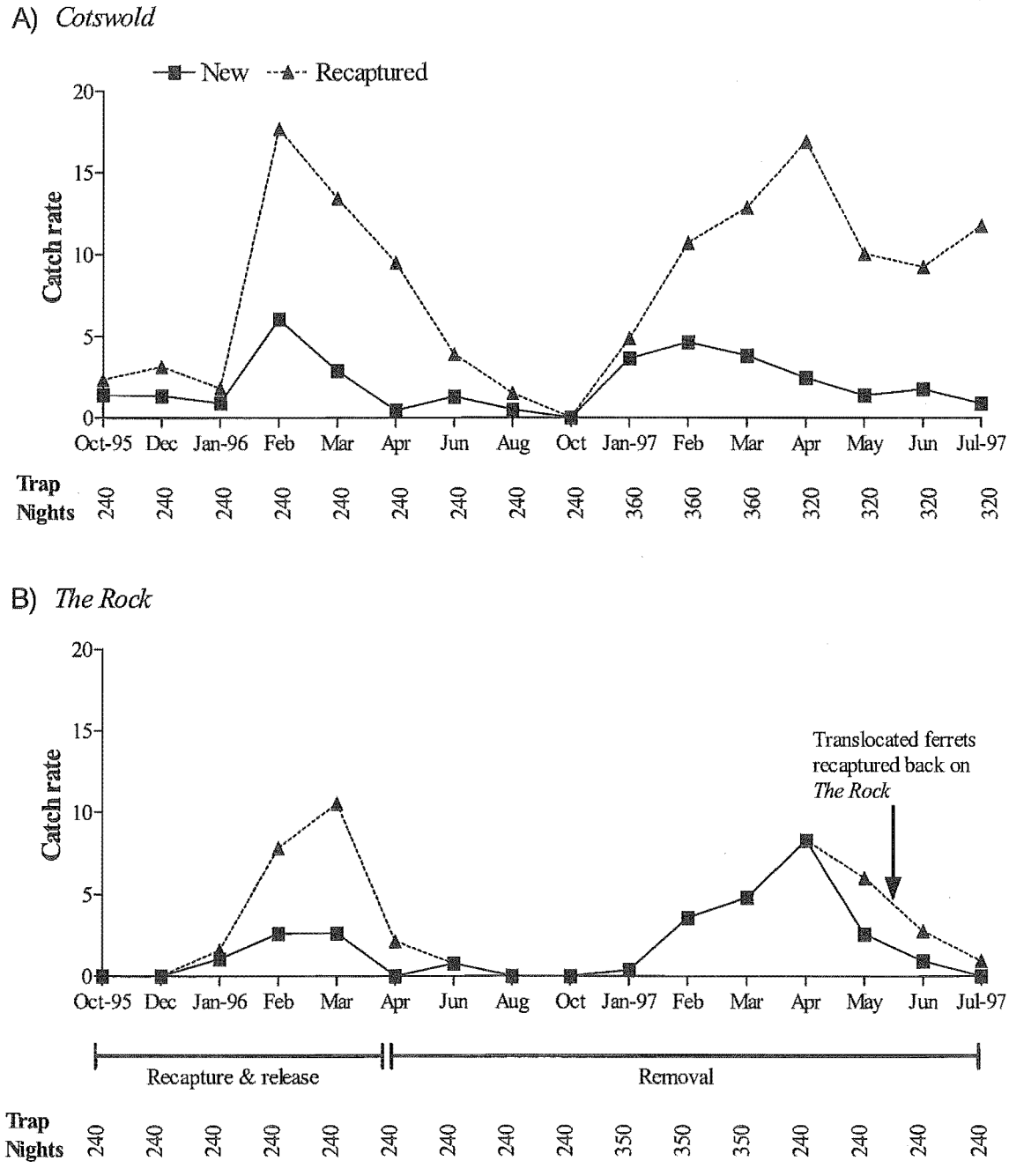


Figure 3.2. Seasonal capture rate (number of ferrets captured per trapping session) of new and recaptured ferrets per 100 corrected trap nights for A) *Cotswold* and B) *The Rock*. Trap nights = number of traps set per trapping session. The recapture rate on *The Rock* from April to July 1997 was for ferrets translocated to *Cotswold* and later recaptured back on *The Rock*.

Table 3.2. Non-target species caught on *Cotswold* and *The Rock* for Years One and Two (HG = hedgehogs (*Erinaceus europaeus*), P = possums (*Trichosurus vulpecula*), MG = magpies (*Gymnorhina tibicen* spp.), B = birds (predominately blackbirds, *Turdus merula* and thrushes *T. philmelos*), H = Australasian harriers (*Circus approximans*), R = rats (*Rattus rattus* and *R. norvegicus*) and stoats (*Mustela erminea*). Mann Whitney Test results for important species shown below table.

	The Rock (Ferrets removed)								**Cotswold (Ferrets not removed)**							
	HG	P	MG	B	H	R	S	All	HG	P	MG	B	H	R	S	All
Year One																
Jan-96	20	7	5	1	4	0	0		7	0	1	3	0	0	0	
Feb-96	33	4	2	1	0	0	0		13	1	2	1	0	0	1	
Mar-96	43	6	2	4	5	0	0		22	1	0	0	5	0	0	
Apr-96	36	4	4	7	0	0	0		18	0	4	1	1	1	0	
Jun-96	0	19	0	0	4	0	0		3	3	0	0	0	3	1	
Totals	132	40	13	13	13	0	0	211	63	5	7	5	6	4	2	92
Year Two																
Jan-97	17	5	0	1	1	5	0		45	0	0	0	0	1	0	
Feb-97	10	8	0	0	0	5	1		26	0	1	0	0	1	1	
Mar-97	10	6	0	0	0	3	1		11	1	0	1	0	2	0	
Apr-97	8	0	0	0	0	0	2		9	0	0	0	1	1	1	
Jun-97	0	7	1	0	2	10	4		0	4	1	0	0	1	0	
Totals	45	26	1	1	3	23	8	107	91	5	2	1	1	6	2	108

Mann-Whitney Results:	**Year One**	**Year Two**
Hedgehogs	$U = 4.5, p = 0.09$	$U = 11, p = 0.75$
Rats	$U = 2.5, p = 0.018$	$U = 2.5, p = 0.018$
Stoats	$U = 7.0, p = 0.21$	$U = 12.5, p = 1$

Although not trapped, wasps (*Vespula vulgaris*) also influenced trap success because they would often swarm around the cages and consume the bait. On *The Rock,* 28% of traps set in March 1996 were affected by wasps and 31% were affected in April 1996. In 1997, only 12% of traps were affected in March and 13% in April. During March and April, no ferrets were ever caught in any of the wasp affected traps yet these traps had the highest ferret catch-rates when wasps were not present. No traps were ever affected by wasps on *Cotswold.*

a) *Habitat and proximity factors that influenced trap success (Cotswold only)*

The estimates of the various effects and standard errors of the full generalised linear model before rescaling are shown in Table 3.3. The full model gave a deviance of 278.16 with 59 degrees of freedom. Proximity to water, type of cover, whether the area around the trap was grazed and whether the trap was set near a fence, building or gully, were all non-significant variables. Three variables were found to significantly influence the capture rate of ferrets (Table 3.4). These, in order of importance, were: 1) whether the trap was set near any cover, 2) whether lagomorph sign was present and, 3) whether the trap was placed along an animal path or track. Although the GLIM model suggests the above three factors have a significant effect on trapping success, only 26% of the residual deviance is explained by the model.

Weather did not significantly influence trap success ($\chi^2 = 0.18$, d.f. = 2, $p = 0.99$). On fine nights, 2.14 new ferrets were captured per 100 CTN on average (mean for all ferrets 7.41 ferrets/100 CTN). On wet nights 2.27 ferrets/100 CTN were caught (mean for all ferrets 10.28 ferrets/100 CTN) while on cloudy nights 1.62 ferrets/100 CTN were trapped (mean for all ferrets 6.59 ferrets/100 CTN).

In Year One, new ferrets were found to be distributed throughout the study area (Mantel randomisation test; $r = 0.04$, $p = 0.81$, n = 30) but in Year Two new ferrets were found to have an aggregated distribution ($r = -0.07$, $p = 0.001$, n = 62). The r-values were low due to a difference in sample size and because both sets of data were highly variable.

3.3.2. Ferret Movement and MCP Areas

The following results only apply to resident sub-adult and adult ferrets during the non-breeding season on *Cotswold.*

Table 3.3. GLIM model variables on a log link scale using a Poisson error term. Shown are the variable estimates and standard errors for (a) the full model and, (b) the revised model.

Model variables	Effect estimate	± 1 S.E.
a) Null Model		
Mean	1.20	0.45
Near water	0.004	0.25
Under cover	0.73	0.28
Cover type 1	-0.08	0.38
Cover type 2	0.07	0.36
Grazed pasture	0.12	0.26
Lagomorph sign	0.40	0.26
Near/in gully	0.23	0.29
Along track/path	0.36	0.24
Near fence/building	0.001	0.27
On slope or flat	-0.10	0.36
b) Revised model		
Under cover	0.72	0.24
Lagomorph sign	0.44	0.22
Along track/path	0.38	0.22

Table 3.4. Contribution of various factors to the catch-rate model. (C = near or under cover, L = presence of lagomorph sign, and T = along an animal track. *t*-values are assumed to have infinite degrees of freedom).

	Residual deviance	Change in deviance	d.f.	*t*-value	P-value
Null model (before rescaling)	278.16		59		
Rescaled model	61.28		59		
Addition of C to model	54.89	6.39	58	2.98	0.003
Addition of L to model	49.46	5.43	57	1.91	0.031
Addition of T to model	47.02	2.44	56	1.69	0.048

a) ***Trap-revealed movements***

The mean straight-line distance travelled by adult female ferrets between traps during a trapping session (over 5 consecutive nights) was 385 m (n = 10, SE = 58 m) while for sub-adult females this distance was 582 m (n = 9, SE = 144 m). In contrast, adult males travelled 491 m (n = 9; SE = 98 m) and sub-adults males travelled 1322 m (n = 14, SE = 312). The mean distance an adult male ferret moved was significantly greater than for adult females ($F = 5.16$, d.f. = 38, $p = 0.028$), and sub-adults, particularly males, travelled further than adults ($F = 9.57$, d.f. = 38, $p = 0.003$). The maximum distance travelled in one night by a ferret was 1370 m for a female and 2015 m for a male. The mean maximum distance travelled between all capture locations during the study by a female was 927 m (SE = 92 m) and for a male was 1572 m (SE = 177 m).

b) ***Trap revealed minimum convex polygon (MCP) areas***

Figure 3.3 shows an example of six MCP areas of female and male ferrets for Year One. MCP areas of the ferrets ranged from 1-306 ha ($\bar{x}$ = 54 ha, SE = 17.3, n = 19) for females and 0.5 -174 ha ($\bar{x}$ = 46 ha, SE = 8.8, n = 23) for males. Although the mean MCP area for females was larger than for males, this was because one female (R131 in Figure 3.3) had an exceptionally large MCP area of 306 ha. The median MCP area for female ferrets was only 29 ha compared to 44 ha for males. Overall, no difference was found between female and male MCP areas ($F = 0.052$, d.f. = 38, $p = 0.82$). However, MCP areas in Year One ($\bar{x}$ = 74 ha, SE = 18.02) were significantly larger ($F = 8.36$, d.f. = 38, $p = 0.006$) than in Year Two .($\bar{x}$ = 30.5 ha, SE = 6.48).

MCP areas where ferrets of the same sex were trapped are shown in Figures 3.4 and 3.5. Several points arise from these figures. Firstly, ferrets of the same sex had MCP areas that overlap. Mean MCP area overlap for males in Year One was 15% (SE = 6%, n = 6) and 12% (SE = 5%, n = 12) in Year Two. Mean female MCP area overlap was 12% (SE = 5%, n = 8) in Year One and 8% (SE = 3%, n = 11) in Year Two. Mean female-male MCP area overlap was 19% in Year One and 14% in Year Two. Secondly, some MCP areas, such as for ferrets 032 and R145, were affected by extreme trap locations. MCP methods can be strongly influenced by peripheral trap locations (Harris *et al.*, 1990). Thirdly, the terrain influenced the spatial distribution of the ferrets. Most ferrets were caught in traps near gullies and along the valleys (an aerial picture of the valleys and gullies is shown in Chapter 1, Figure 1.4). Fourthly, no resident ferrets were trapped near the main plantation area in Year Two (the plantation is shown on Figure 1.2 Chapter 1). Finally, in Year Two

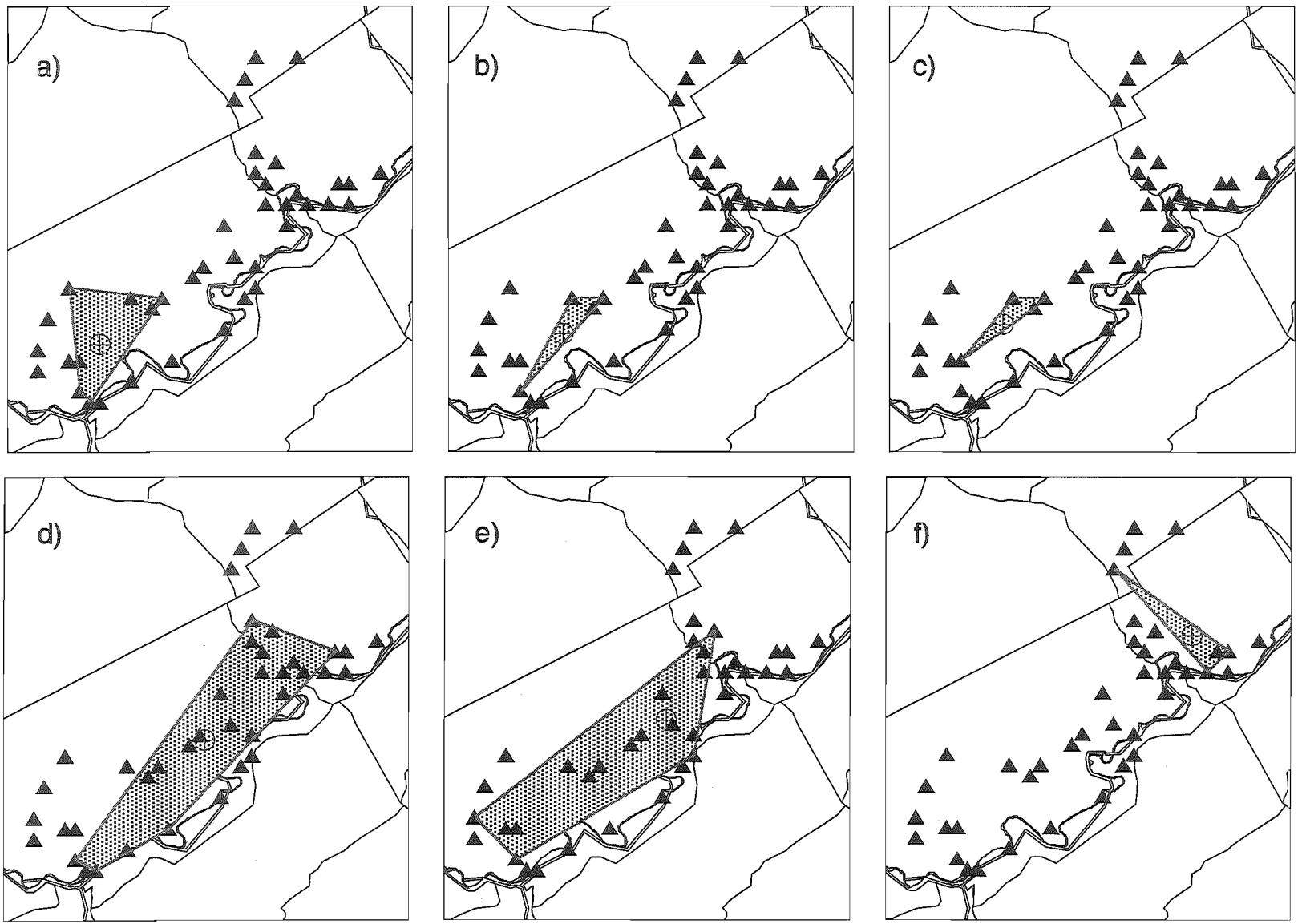


Figure 3.3. Trap sites and MCP areas of six male ferrets (a = R105, b = R107, c = R111, d = R143, e = R180, f = R195) in Year One. (circle with cross hairs = arithmetic mean. Triangles = trap sites. Note only 1st 40 traps shown).

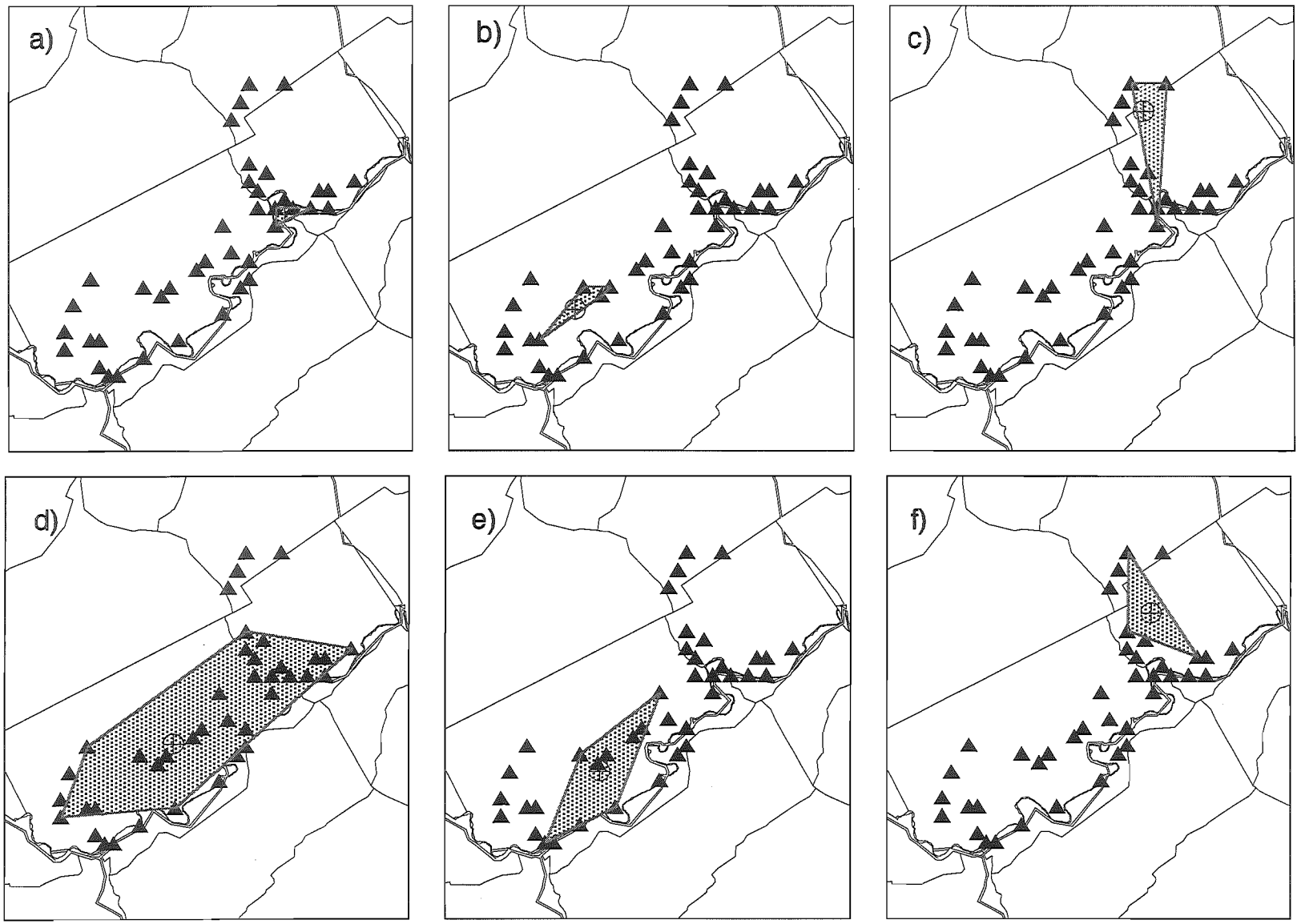


Figure 3.3 (cont.). Trap sites and MCP areas of six female ferrets (a = R102, b = R111, c = R114, d = R131, e = R133, f = R188) in Year One. (circle with cross hairs = arithmetic mean. Triangles = trap sites. Note: only 1st 40 traps shown).

Figure 3.4. Overlap of six male ferret MCP areas in Year One

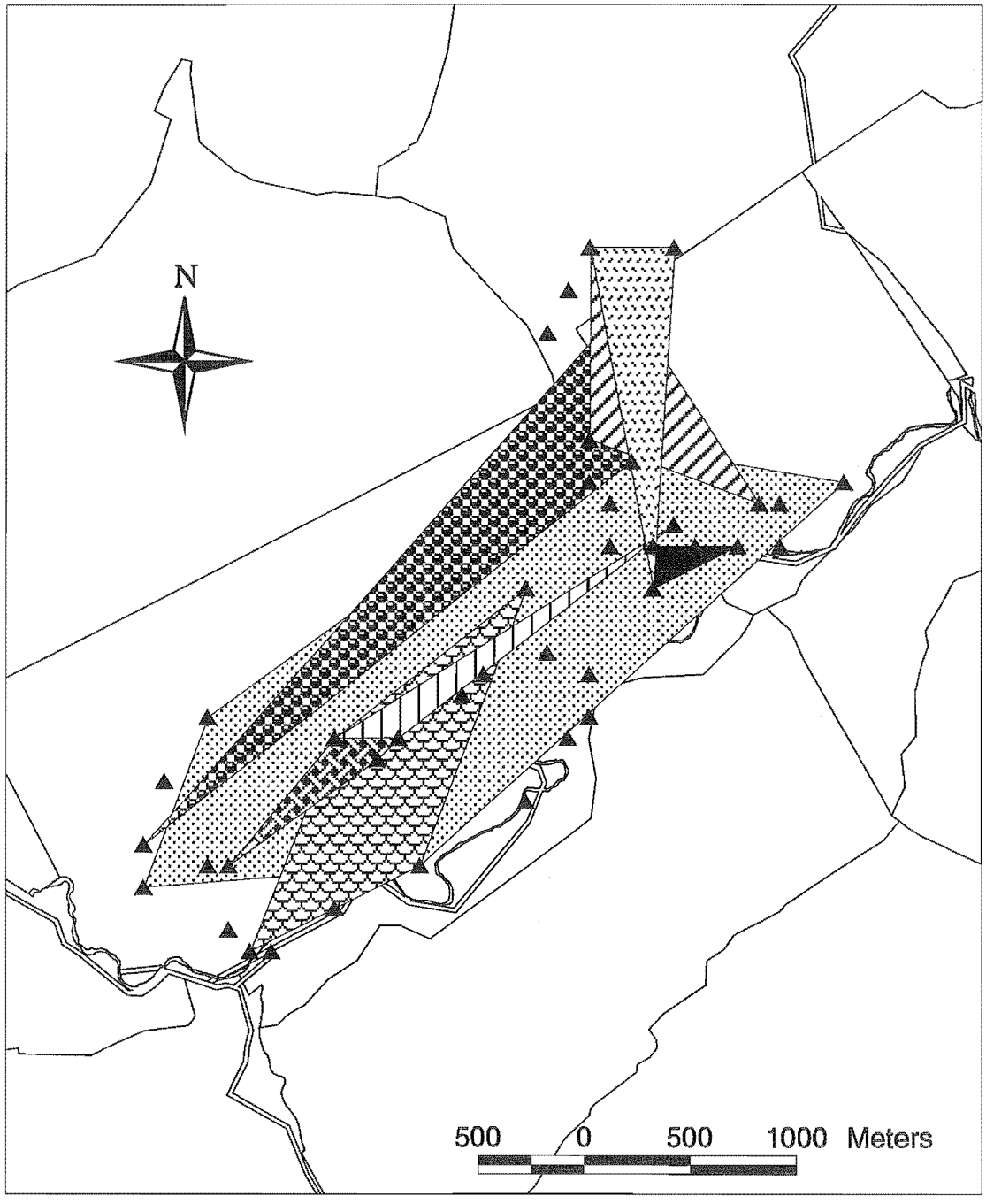


Figure 3.4 (cont.). Overlap of eight female ferret MCP areas in Year One

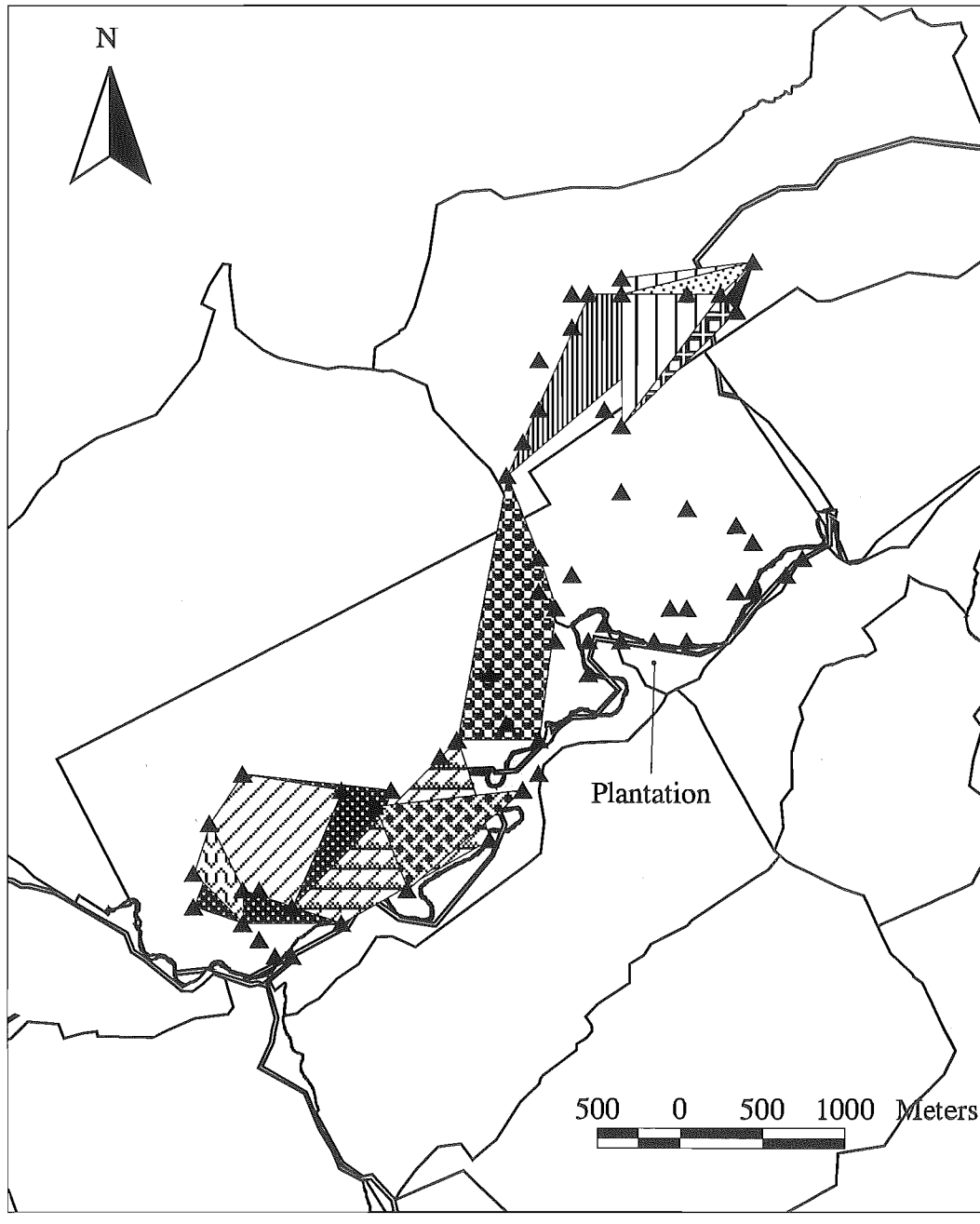


Figure 3.5. Overlap of eleven male ferret MCP areas in Year Two. Note: distribution into two main patches, northern and southern groups

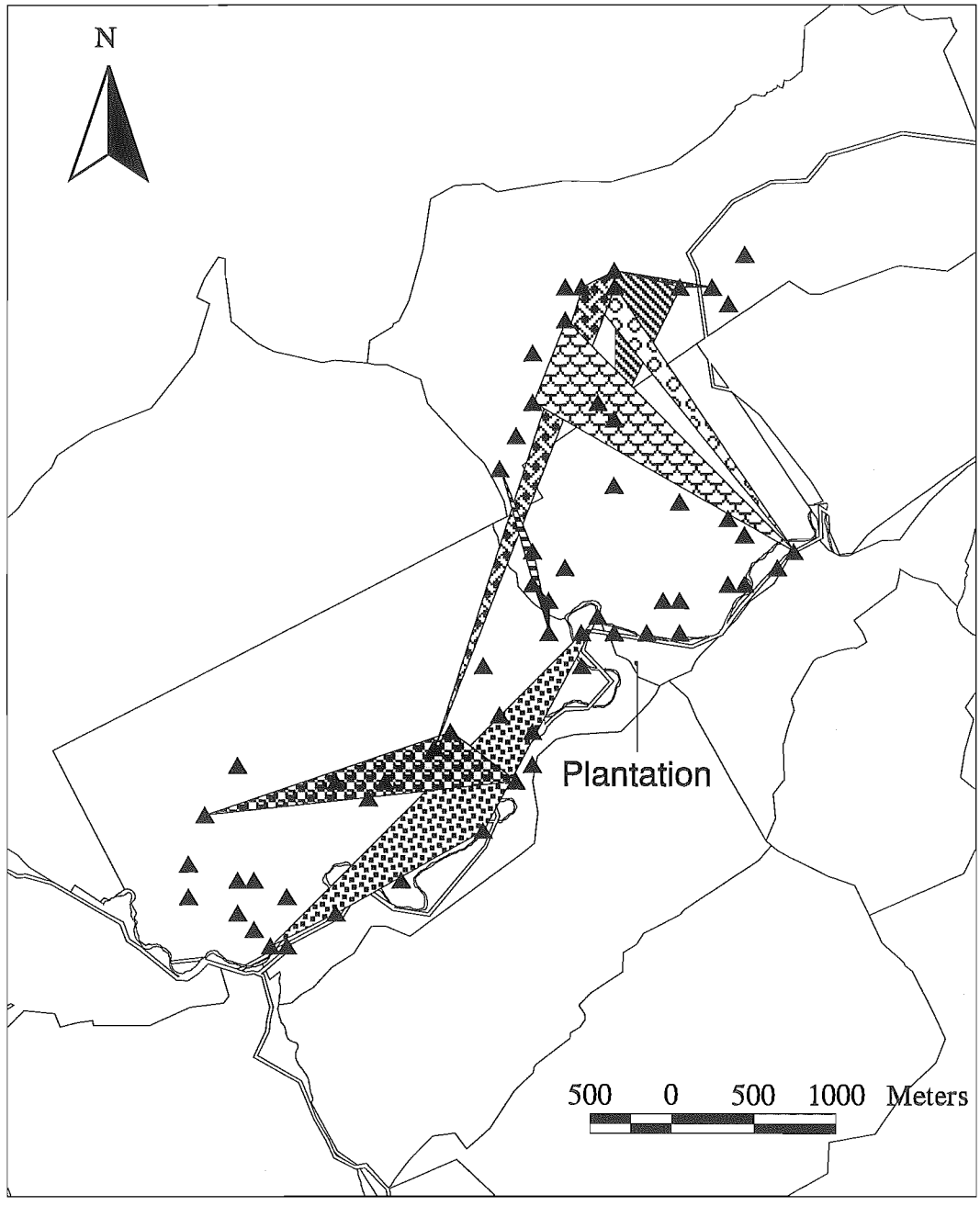


Figure 3.5 (cont.). Overlap of nine female ferret MCP areas in Year Two. Note distribution into two main patches.

but not Year One, the spatial pattern of ferret activity was divided into two main patches. These patches are: 1) ferrets 028, 045, 047, 026 060 (southern group) and 2) ferrets 036, 110, 169, 108, 091 (northern group) which were linked by ferret 051.

During the study, different ferrets were caught in the same trap on successive nights. On 23 separate occasions, a male ferret was captured on one night and a different male ferret was caught in the same trap the following night. On seven occasions, three different males were captured in the same trap on successive nights. Different female ferrets were also recorded in the same trap on successive nights on 13 occasions, and three different females were caught in the same trap on four occasions. This pattern of repeated recapture was not exclusively a gender phenomenon. On 11 occasions, a male ferret was first captured and a female was captured in the same trap the following night. On 10 occasions, a female ferret was captured first followed by a male. An example showing overlapping MCPs of a male ferret and five female ferrets is shown in Figure 3.6.

Ferrets released from a trap would often be recaptured in the same trap the following night. This occurred on 14 occasions. Twenty-one ferrets were trapped the following night in the next closest trap (in a radial distance from the original trap) and 23 ferrets were caught the following night in a trap more than three traps away.

c) *Site fidelity and homing ability*

Monte Carlo site fidelity simulations revealed that 71% (n = 7) of female ferrets in Year One had strong site fidelity whereas only 33% (n = 6) of male ferrets had a strong attachment to the area in which they were trapped (Figure 3.7). In Year Two, all females (n = 8) had strong site fidelity and site fidelity also increased for the males to 67% (n = 15). An example of an extrapolated movement path that did not display any site fidelity is shown in Figure 3.8. Only two ferrets out of 143 trapped on one study site were ever trapped on the other study site. Both ferrets (019 and 068) were males from *Cotswold.* Ferret 019 was trapped twice in quick succession on *Cotswold* before it was trapped a month later and killed on *The Rock.* Ferret 068 was translocated back to *Cotswold,* released in the same area where it was originally caught and was later trapped and killed back on *The Rock.* Before the translocations, no ferrets trapped on *The Rock* were ever trapped on *Cotswold.*

Of the 14 ferrets translocated from *The Rock* to *Cotswold,* eight were recaptured on *The Rock* and two were recaptured on *Cotswold.* Five of the ferrets recaptured on *The Rock* were trapped within 300 m of their original capture site (four of these ferrets were females).

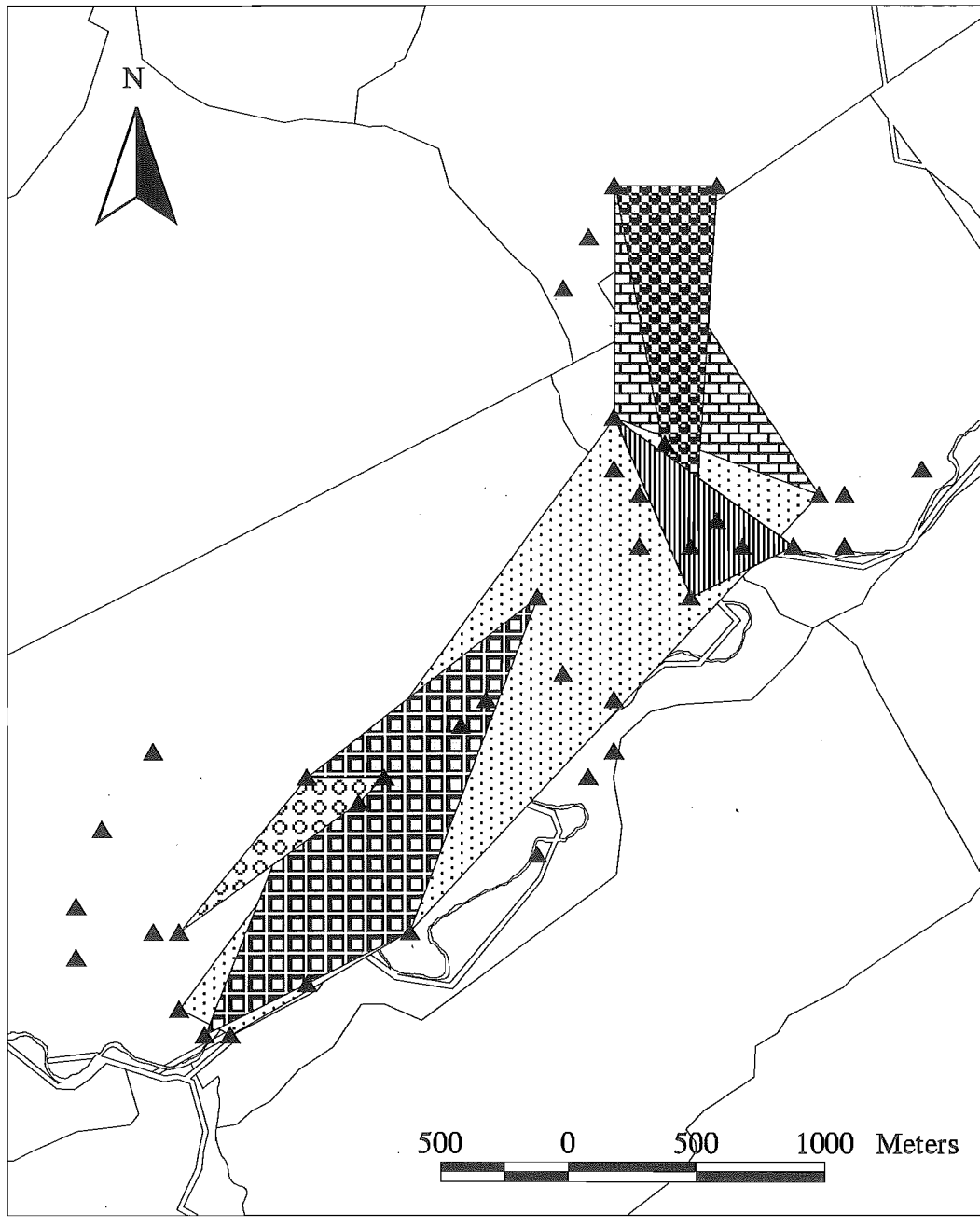
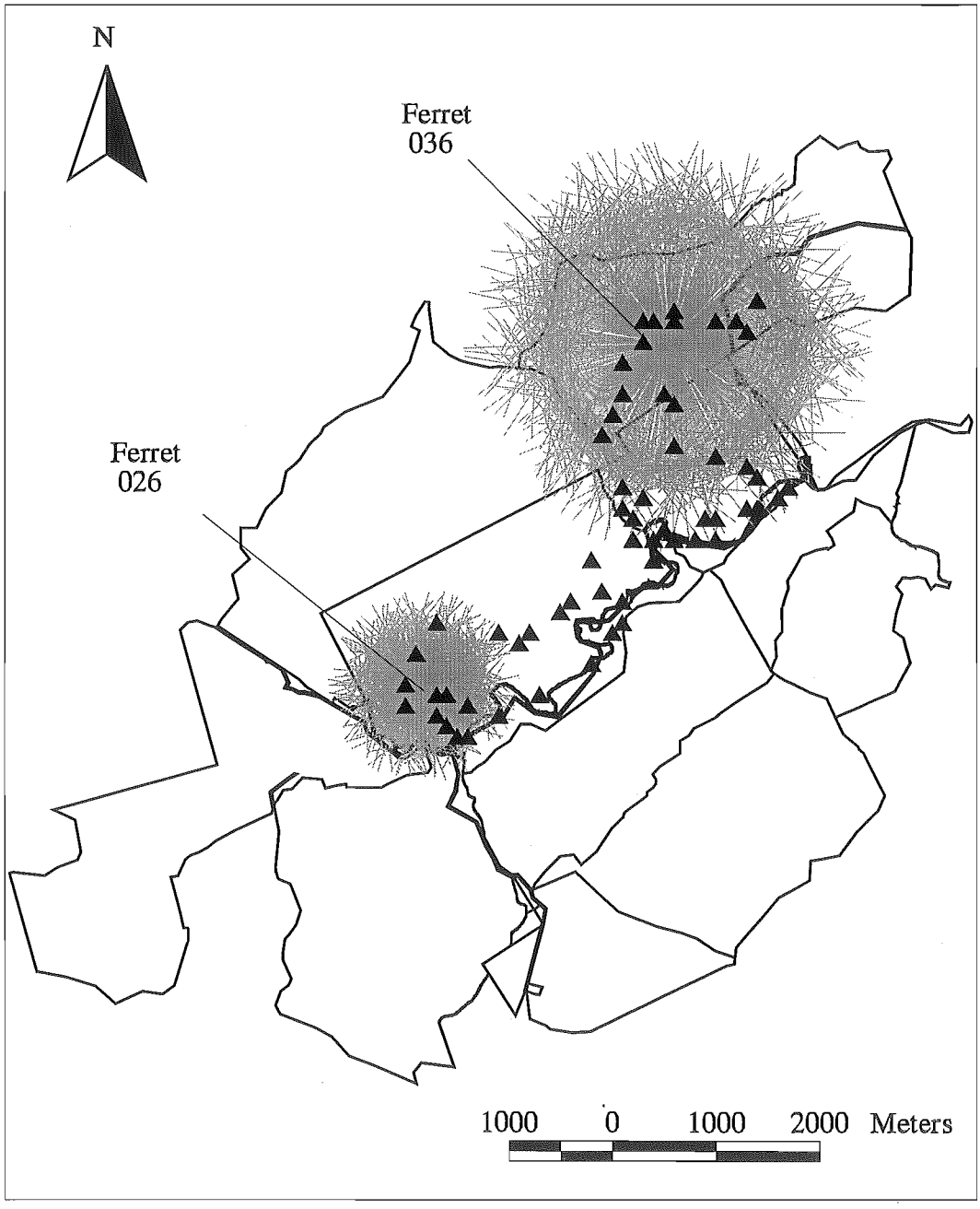


Figure 3.6. Example of a male-female MCP overlap for Year One. Five females are shown and the male ferret is R143.



Legend

Triangles = layout of trap sites

General outline = farm boundaries

Figure 3.7. Site fidelity examples for ferrets 026 and 036. Gray lines extrapolate the actual movement path of each ferret based on 1000 iterations of the ferrets trap histories.

Legend

Triangles = trap sites

General outline = farm boundaries

Figure 3.8. Site fidelity example for ferret R143. Gray lines extrapolate the actual movement path of R143 based on 100 iterations of R143's trap history

The other four ferrets translocated to *Cotswold* were never captured again (three of the four were males). To further test their homing ability, four (2 female and 2 male) of the eight ferrets recaptured back on *The Rock* were released back onto *Cotswold* and of these, three were recaptured back on *The Rock.* The fourth ferret (a male) was never captured again.

3.4. Discussion

3.4.1. Trap Success

Ferret capture rates varied throughout the year. Few ferrets were caught in late winter, spring or early summer (August-December), most were trapped from January-July. This pattern was also observed by several other researchers in New Zealand. From May 1995 to May 1997 in another North Canterbury study, trap success varied from 5.6 new ferrets per 100 corrected trap nights (CTN) in summer to 1.3 ferrets per 100 CTN in autumn (Caley *et al.,* 1998). During a 28 month study on *The Rock* when 65 ferrets and 25 cats were caught, trap success for cats and ferrets ranged seasonally from 1.6 -4.8 predators per 100 CTN (Robson 1993). Capture rate ranged from 5.1-21.1 new ferrets/100 (uncorrected) trap-nights in a study at Palmerston in Otago, an unusually high range compared with 21 other nearby sites in Otago (0-10.6 ferrets/100 CTN: Ragg 1997).

Trap-lines designed to monitor populations are unrepresentative if there is a strong sex bias because they will not provide true samples of the population (Pollock *et al.,* 1990; King *et al.,* 1994). Sex biases in mustelid populations are thought to be a function of trap layout (Lockie 1966). In sexually dimorphic mustelid species, males have larger home ranges than females (Buskirk and Lindstedt 1989). Consequently, males have greater opportunity to encounter more traps when searching for food or mates. Although more male ferrets were captured than females, no statistical evidence of any sex bias was apparent in this study (see Chapter 2). The actual sex ratio of many mustelid species is thought to be 50:50 (Powell 1994) and is not as highly skewed towards males as some trapping results suggest. Indeed, the sex ratio of ferrets trapped at Pukepuke Lagoon alternated between years and in the final analysis the sex ratio came out to be roughly equal (Moors and Lavers 1981).

Capture rates also varied between traps. The presence of vegetation cover near a trap was found to be the most influential factor increasing trap success; however, the type

of cover was not significant. Lagomorph sign was the second most influential factor. Ferrets primarily hunt rabbits in their dens and although rabbits feed in the open pasture at night they seek vegetation cover during the day (Gibb 1977; Fraser 1992). Most lagomorph sign was found in the open but not far from cover. In the MacKenzie Basin, ferrets were observed to hunt rabbits more frequently in areas with abundant vegetation (Pierce 1987; Pascoe 1995).

During summer, polecats in Switzerland used burrows, woodpiles and dense vegetation as resting sites and in winter they slept mainly inside farm buildings, particularly barns, where it was warm and dry (Weber 1989b). However, few ferrets were captured in farm buildings in North Canterbury. Possibly this is because: a) winter temperatures in North Canterbury are not as extreme as they are in Europe and so farm buildings are not needed for warmth, or b) the density of farm buildings in North Canterbury is not as great as in Europe, or c) most farm buildings in North Canterbury are hay-barns which are disturbed too often for a resting site. Nevertheless, Ragg (1997) found that ferrets in Otago did use farm buildings as den sites, not because they were seeking warmth and shelter, but because of the local rodent populations.

The third factor that improved trap success was setting the trap along an animal pathway or track. Rabbits prefer feeding sites where the grass is short, but only if they can escape to an area that provides them with cover. Therefore, rabbits often create runways (animal paths) from their resting sites in the gullies to their feeding grounds in the open pasture (Fraser 1985). Placing a trap on a track, especially if it was near a gully and lagomorph sign, increased the likelihood of trapping a ferret.

Although three factors significantly influenced trapping success they only explained 26% of the model deviance. This implies that a significant amount of the variation in the catch rate of ferrets is caused by other factors not included in the model.

Many ferrets were trapped near gullies, and although only just insignificant, gullies are important to ferrets for several reasons; a) prey often rest in them, b) gullies provide cover when hunting or moving and, c) they provide a refuge area for den sites. In a microhabitat study in Switzerland, polecats avoided areas of bare ground which would expose them to larger predators. Instead, they chose microhabitats with some form of shelter from sight (Weber 1988). However, ferrets in North Canterbury were often observed out in the open at night away from the sheltered gullies (*pers. obs.*) which could

explain why the model found gullies not significant. Although the chances of observing a ferret in a gully are reduced because of the vegetation, most ferrets observed were searching burrows and stops (short tunnels <1 m where young rabbits are reared). Robson (1993) in a study on juvenile rabbits, found that the majority of breeding stops were dug in areas of open pasture rather than in the sheltered gullies. Thus, if ferrets are to hunt young rabbits in stops they must leave the gullies and move out into the open. On many occasions ferrets were observed several hundred metres away from cover; however, this may not be as risky in New Zealand because ferrets have few predators other than people hunting pests and, if they are disturbed, they can quickly escape down rabbit holes.

Surprisingly, one factor that did not influence trap success was the presence of water, especially during times of drought. Ferrets in a large outdoor semi-natural enclosure were observed to drink on average 10 times a day (see Chapter 6), and this would suggest that placing traps near water is a good tactic. In Europe, waterways are important for polecats as a route of dispersal (Heptner 1964), and they are often caught or observed along stream tributaries and rivers (Saint-Girons 1974). Polecats in Poland during the winter predominately lived and moved along the side of streams or rivers because this was where most of their prey were concentrated (Jedrzejewski *et al.*, 1993; Sidorovich *et al.*, 1996). Accordingly, polecats in some regions concentrated their hunting efforts around waterways because they specialised in eating frogs (*Rana dalmatina*) and toads (Weber 1989a; Lodé 1996b). However, ferrets drink only a small amount of water and they can drink all they require from even the smallest puddles.

Low trap success in late winter-early summer is an enigma. Ferrets, especially females, are difficult to trap in spring (Ragg 1997). An abundance of juvenile rabbits (prey) during this period may explain why ferrets do not take bait set in traps. In a capture-recapture study on feral house mice (*Mus domesticus*) one of the six explanations proposed for the low trappability rates was an excess of food near the traps (Krebs *et al.*, 1994). Lagomorphs, the main prey species in North Canterbury, are capable of breeding year round but produce their biggest litters in spring (Bell 1977). This increase in lagomorph availability in spring corresponded with a large decline in trap success. Yet, in a study researching the mortality rates of juvenile rabbits on *The Rock*, most juvenile rabbits were killed by predators in autumn rather than in spring when there is excess of available prey (Robson 1993). One possible explanation for this is that ferret numbers are indeed low in spring and after recruitment in summer they have a greater impact on juvenile rabbits in

autumn. One estimate of the mean life expectancy of polecats in Europe was 8.1 months (Walton 1977). If the same is true for ferrets in New Zealand, and their mean birth date is approximately 30 October (see Caley *et al.*, 1998), then in theory, only a few ferrets will survive to have an impact on the juvenile lagomorphs in spring. This question has not yet been satisfactorily answered, and more work to resolve this issue is required (see Chapters 2 and 6).

Although the trap-catch was adjusted to account for non-target species and sprung traps, these components effectively reduced the numbers of traps available to trap target species. This was particularly evident on *The Rock* where up to a quarter of all traps during summer and autumn were affected. The most troublesome species were hedgehogs, possums and wasps. To reduce the effect of these animals on the catch-rate, possums were removed and poison was applied to the wasp nests near the affected traps. Unfortunately, the poison did not decrease the wasp problem and it was deemed inappropriate to remove the hedgehogs out of the area because they are potential hosts for Tb (Lugton *et al.*, 1995).

A major concern for bird conservationists raised by my study was the increase of rats and stoats on *The Rock* when ferrets, as well as cats, where removed (Table 3.2). This increase was not observed on *Cotswold*, the site where predators were not being removed. An increase in rat numbers may be more detrimental for wildlife than the presence of cats (Fitzgerald 1990b). Ferrets and cats both prey upon rats (Roser and Lavers 1976; Langham 1990) but it is cats which probably have the biggest impact on rat and stoat numbers (Innes 1990; Moors 1990). A study in the Orongorongo Valley, near Wellington, found that the rat population increased four-fold when cats were reduced over a three year period (Fitzgerald and Karl 1979). The observed increase in rat and stoat numbers help support the view that if larger predators are removed, smaller, and perhaps more troublesome predators like rats and stoats, may create even greater conservation problems.

3.4.2. Ferret movements and spatial distribution

The mean distance a ferret moved varied according to sex and age. Adult males moved further than adult females and sub-adult males moved more than twice the distance of sub-adult females. Male ferrets are thought to move greater distances than females because they are physically larger and because they have larger territories and home ranges (Moors and Lavers 1981). Home range estimates for ferrets in New Zealand all confirm that males have

larger home ranges than females (Moors and Lavers 1981; Ragg 1997; Norbury *et al.*, 1998b); however, the size of the home ranges varied depending upon the method used. For example, Moors and Lavers (1981) trapped in a dune/swamp/pasture habitat and found that females had a home range of 12.4 ha and males had a home range of 31.3 ha. Meanwhile, in a large-scale project where ferrets were radio-tracked in a dry, tussock grassland, male ferrets had mean home ranges of 102 ha and females ferrets had home ranges averaging 76 ha (Norbury *et al.*, 1998).

Estimating the size and shape of a home range can be problematic because home ranges invariably change with respect to sex, status, season and prey abundance (MacDonald 1983; Harris *et al.*, 1990). Home range areas are where an animal learns sources of food and water, resting and den sites, and look-out positions and escape routes (Delany 1982). They are also areas of ground which are frequently patrolled (Riney 1982). Unfortunately, because much of this home range information was unknown in this study, it was decided not to define the MCP areas as home ranges. Instead, MCP areas were used only to indicate the presence, distribution and movements of individual ferrets in an area. Furthermore, home range size cannot be accurately estimated using trapping because range information is influenced by the number of traps available, grid size and shape, edge effects, individual differences in trappability and where the traps are situated (Ragg 1997). Nevertheless, one advantage of trapping is that it provides physical proof that the ferret was at a particular site whereas radio-tracking locations can occasionally be biased (Harris *et al.*, 1990)

Often when prey numbers increase, smaller home ranges result (Herrmann 1994). Lagomorph numbers in North Canterbury increased dramatically in Year Two (see Chapter 4) and ferret MCP areas declined compared to the MCP areas recorded in Year One. The costs of defending a territory can be high (Brown 1982), and smaller home ranges mean that less time and energy is spent foraging, and maintaining a constant body temperature (Karasov 1981). In addition, rather than expending energy in territorial defence, when sufficient prey were available the ferrets reduced their areas of activity. This was predicted by Sandell (1989) for solitary carnivores where home range size is determined by food availability.

Powell (1993) predicted that when prey populations increase, territories of sexually dimorphic mustelids should decrease and their ranges should overlap extensively. That is, they change from exhibiting intrasexual territoriality within sexes to becoming non-

territorial when prey abundance is high. With the increase in lagomorph numbers MCP areas declined in Year Two, but proportionately, the amount of MCP area overlap did not change between years. However, temporal overlap was evident in my study as different ferrets, of either the same sex or different sexes, were often caught in the same trap on consecutive nights. This suggests that the ferrets in North Canterbury were not defending any exclusive territorial areas when prey densities were high.

In another population of trapped ferrets, intrasexual territoriality was observed as members of the same sex excluded each other from their home ranges while members of different sexes had overlapping home ranges (Moors and Lavers 1981). But once their prey population increased to unusually high levels, members of the same sex had overlapping home ranges, especially the females. Likewise, intrasexual territoriality was also observed with ferrets held in captivity as they shared their dens less often within sexes than between sexes (Medina-Vogel 1998). However, when food was given at twice the normal rate, these captive ferrets reduced their territories and had extensive range overlap.

Non-territorial behaviour was also observed in two populations of ferrets monitored using radio tracking. Ragg (1997) found the mean range overlap of ferrets in Otago was 9.2% for males, 5.2% for females and 13% for male-females. Similarly, ferrets in Central Otago and the MacKenzie Basin had even larger overlapping mean home ranges: 13-34% for males overlapping other males, 11-23% for females overlapping other females and 12-31% for males overlapping female ranges (Norbury *et al.,* 1998b). Medina-Vogel (1998) suggested the reason that intrasexual territoriality was not found by Ragg (1997) was because of the high population density of ferrets, and that density *per se* should not affect intrasexual territoriality. Norbury *et al.*, (1998) suggested that high prey densities probably explained why intrasexual territoriality was not observed in their study.

Ferret spatial distribution varied from one year to the next. In Year One, no spatial aggregation was evident but in Year Two, some spatial aggregation was present as most ferrets were trapped in two main patches. Brown and Litvaitis (1995) suggested that the distribution of essential requisites such as den sites, prey, and water will cause predators to concentrate in certain patches of landscape. Predators, such as red foxes (*Vulpes vulpes*), are also known to select habitats with dense vegetation that support high numbers of lagomorphs (Halpin and Bissonette 1988). Although both patches had high lagomorph numbers with good cover and access to water, other areas on *Cotswold* also had high concentrations of prey and plenty of water but were not occupied by ferrets.

The distance between the two main patches was over 3 km and only two ferrets (032 and 051; Figure 3.5) were ever caught in both patches in Year Two. However, 051 was only captured on the periphery of the two patches and 032 was captured several times in the northern patch, once in the southern patch and then recaptured back in the northern patch. In Year Two, many cats were caught in the area between the two main patches but only a few new ferrets were ever captured. This contrasted with Year One where most new ferrets were caught in this area and only a few new cats. Interestingly, the area between the two main patches had the highest concentration of lagomorphs (in both years) followed by the northern patch and then the southern patch; so it is puzzling as to why only a few ferrets were caught between the two main patches in Year Two. Unless, there was an excess of live prey and these were eaten in preference to bait provided in the traps.

Intraguild predation between cats and ferrets may be responsible for the low ferret catch-rate between the two patches, but this implies that cats can actively exclude ferrets from a large area when there was an abundance of prey. This would seem to be an unusual strategy, especially as both cats and ferrets were frequently captured in the two main patches. In nine studies on cat and ferret diet in New Zealand, only one reported the presence of an intraguild predator in the diet (Ragg 1998; see Chapter 4). Finding only cat remains without the presence of maggots in ferret scats is extraordinary (as this implies that a ferret is capable of killing a cat) as most intraguild predation occurs in ecosystems with size-structured populations by generalist predators that are larger than their intraguild prey (Polis *et al.,* 1989). Lack of den sites is another possible explanation of why ferrets were not captured between the patches, but again, this is puzzling as ferrets had been frequently captured in this area the year before. No land or farm management practices changed in this area between the two years and a stream constantly flowed between the two patches.

As part of a Tb management programme every farmer in the Omihi district was encouraged to trap ferrets (Oliver 1996). Many farmers set their traps on the boundary between their property and the study site. Consequently, 12 tagged ferrets were caught, all in Year One. One male ferret managed to get through this cordon and was later trapped 5.2 km away from the study site (M. Gilbert *pers. comm.*). This was the maximum distance a tagged ferret was recorded to have dispersed during this study. Within the study site itself the maximum distance a juvenile male moved was 2 km which was similar to that found by Wilcox (1978, cited in Blandford, 1987) in Britain for polecats. However, ferret dispersal

has been recorded up to 29 km in New Zealand (Pierce 1987), and 35 km for polecats in Britain (Poole 1970, cited in Blandford, 1987).

Site fidelity was weaker in Year One when the ferrets were randomly distributed but was stronger in Year Two when the ferrets had more aggregated MCP areas. Site fidelity was also stronger for females than males. Although rejecting the null hypothesis indicates strong site fidelity, it should be pointed out that low sample size and the use of trap location data to identify the actual movement paths of the ferrets, may mean the null hypothesis was rejected when in fact it was true (a Type 1 error). Nevertheless, my results corroborate many of the findings of this study. In a study of Egyptian mongooses (*Herpestes ichnuenmon*), adult males would patrol their territories more often than adult females and their patrols included more area than expected from random; thus, males exhibited less daily site fidelity than females (Palomares 1994). Males would also exhibit less site fidelity if they adopted a roaming behaviour in search of receptive females rather than staying in one location and defending one or more females (Sandell and Liberg 1992).

The homing ability of ferrets appears to be quite strong as 64% of those translocated to another farm were recaptured near their original capture site. To my knowledge this has not been tested on ferrets before. Animals commonly find their way back to the same area, often to precisely the same home range (Riney 1982). Five of the translocated ferrets were caught within 300 m of their original trap site. Although the translocation site (*Cotswold*) was just over 1 km in a straight line from *The Rock*, only 2 out of 143 ferrets (both males) naturally dispersed from one site to the other. Both males were caught near the entrance of *The Rock* not far from the road. Ragg (1997) found that ferrets were often associated with the ungrazed verges near roads. The farm between the two study sites formed a natural geographical barrier as it had a high ridge (>400 m).

These movement results raise the question: If ferrets exhibit strong site fidelity and the resident population is stable should these animals be targeted for a removal programme if Tb is not present in an area? By removing a stable population of ferrets that do not roam, it could be an invitation for transient ferrets (mainly young ferrets?) to move into the area vacated by the residents. This movement into a sink area could possibly provide the catalyst for a Tb epidemic, if transients infected with Tb move to non-Tb areas. Research into ferret population stability and reinvasion rates should be carried out in an area where Tb is not present to determine whether ferrets move into sink areas.

In conclusion, although ferrets are inquisitive and may be captured if a trap is placed inside their territory, understanding what habitats they frequent, where they are likely to roam and what they are likely to eat should improve trapping success. This information can be used to identify likely habitats and "hot-spots" where ferrets may be caught. As the purpose of a trapping programme is to maximise the amount of information (or ferrets captured) for a given cost, then a stratified random sampling system may be a preferable alternative to the standard systematic or simple sampling methods currently used. By allocating the trapping effort into key habitats or strata, large gains in trapping success and precision may result, especially if more information about ferret movement patterns, habitat use, and prey distribution are made available.

The low capture rates during winter and spring also suggest that the timing of a trapping programme is also important. If the requirement of a trapping programme is to reduce ferret numbers, then trapping ferrets before they breed may be more effective. However, this is normally when ferrets are at their most difficult to trap. Therefore, the reasons for this lack of trap success during winter and spring requires further investigation. Admittedly, trapping is not an exact science because the behaviour of ferrets is unpredictable; thus, what is needed is a detailed study of their behaviour, especially during the breeding season. Nevertheless, my study adds further evidence to that provided by Ragg (1997) and Moller *et al.*, (1996) about when and where to target ferret populations for future trapping programmes.

Chapter Four

Comparing the dietary habits of cats and ferrets on North Canterbury farmland with other cat, ferret and polecat populations.

4. Abstract

Both cats (*Felis catus*) and ferrets (*Mustela furo*) were introduced by Europeans into New Zealand. Both cats and ferrets are known to carry *Mycobacterium bovis* (Tb) and questions about how they contract this disease has lead to several studies on their diet. My study investigates what prey species cats and ferrets consume and the reason for the dominance of lagomorph (rabbits, *Oryctolagus cuniculus* and hares *Lepus europaeus*) in their diet in North Canterbury. I also compare the diets of New Zealand cats and ferrets with those of other populations overseas. It was found that, even though cats and ferrets use different hunting strategies, lagomorphs were their staple prey in North Canterbury. Prey availability and prey preference as well as differences in habitat are all hypothesised to influence cat and ferret diet. Few sex and age differences were found in the diet of ferrets and cats in North Canterbury. While the North Canterbury results reflect those of other New Zealand studies, in that both ferrets and cats mainly consume lagomorphs, it was found that polecats in Europe, as well as feral cats in Australia have a wider range of suitable prey and a more broader diet. Unlike overseas habitats, New Zealand farmland lacks suitable alternative prey and this may explain the narrow diet of both cats and ferrets. Consistently, the limited range of suitable prey on island habitats was also reflected in the narrow diet of cats on islands. Even with the large increase in lagomorph numbers seen in North Canterbury in the second year of study, the diets of both predators remained the same, showing that these predators are unable to regulate lagomorphs once their numbers cross a certain threshold. This total reliance on lagomorphs suggests that one way to control ferrets is to reduce lagomorph numbers, thereby depriving ferrets of their main prey. Nevertheless, while Tb is thought to be contracted as a result of eating infected meat, few Tb host species were found in the diet of either cats or ferrets in North Canterbury, so the question of how ferrets contract Tb still remains unanswered.

4.1. Introduction

New Zealand's terrestrial mammalian fauna is most unusual. Virtually all of it has been deliberately introduced since European settlement. Prior to these introductions, the only terrestrial mammals were three species of bats (Daniel 1990). Initially, the first settlers from Polynesia introduced kiore, the Polynesian rat (*Rattus exulans*) and kuri, the domestic dog (*Canis familiaris*), while the European settlers that followed intentionally introduced both domestic and wild species for food, fur and sport, such as sheep (*Ovis aries*), pigs (*Sus scrofa*), rabbits (*Oryctolagus cuniculus*) and possums (*Trichosurus vulpecula*). Several other mammals that accompanied colonisation included European rats (*R. rattus* and *R. norvegicus*), mice (*Mus musculus*), and house cats (*Felis catus*: King 1990).

Rabbits became an agricultural pest soon after their introduction to New Zealand. To control rabbit numbers, weasels (*Mustela nivalis*), stoats (*M. erminea*) and ferrets (*M. furo*) were also introduced. The decision to introduce mustelids was based on the assumption that they were specialist rabbit predators. In 1867, ferrets were first introduced from Britain by the Canterbury Acclimatisation Society, while both stoats and weasels were introduced in 1884 by the New Zealand Government (Wodzicki 1950). As a biocontrol experiment the introduction of mustelids failed, and rabbit numbers continued to rise (Gibb and Williams 1994).

Following their introduction, no formal mustelid diet studies were undertaken; however, biologists believe that instead of hunting rabbits, mustelids switched to hunting native species (Wodzicki 1950). As a result, mustelids themselves soon became regarded as pests (Lavers and Clapperton 1990). Even though cats and ferrets were implicated in the decline of New Zealand's native fauna, it was not until recently that the diets of these predators came under scientific scrutiny (King 1984; Fitzgerald 1988). The key finding in most contemporary studies is that lagomorphs (rabbits and hares, *Lepus europaeus*), rather than native birds, are the main prey species eaten by ferrets and cats (Gibb *et al.*, 1978; Smith *et al.*, 1995; Ragg 1998).

With the recent discovery that ferrets carry *Mycobacterium bovis* (Tb) there has been intense interest in what ferrets (and cats) are eating (e.g., Smith *et al.*, 1995; Ragg 1998). Farmers are mostly concerned with the threat that infected ferrets pose on their livelihoods. Epidemiological studies of *M. bovis* infection in ferrets suggest that eating infected prey or carrion may be a common route of *M. bovis* infection (Lugton *et al.*,

1997a; Ragg 1997). Therefore, it is important to verify what they are eating in North Canterbury.

One hypothesis for the predominance of lagomorphs in cat and ferret diets is the lack of suitable alternative prey. Fifty-four mammalian species were introduced into New Zealand, but most were comparatively large. Only nine species under 1 kg are, or have been present, including bats and extinct species, compared to Britain's forty-one species under 1 kg (King 1990). This low diversity of small prey meant that cats and ferrets, which are relatively small predators themselves, either had to specialise in hunting the few introduced species, mainly rats, mice and young rabbits, and/or switch to consuming the native fauna.

Ferrets, by virtue of their long lithe bodies, are able to hunt prey under circumstances different from those determining the hunting success of cats. Ferrets are able to manoeuvre into tight crevices and underground burrows to hunt, while cats normally stalk and pounce on their prey when they are above ground. Over a ten year study in the Wairarapa, cats were never observed to dig out juvenile rabbits in an underground nest even though they could detect their presence. Instead they would wait until the young rabbits emerged (Gibb *et al.,* 1978). Another strategy used by cats is to utilise their agility to stalk prey in trees. In contrast, ferrets, like their relative the polecat, are poor climbers and are restricted to hunting prey on or below the ground. Cats hunt both during the day and at night by sight whereas ferrets hunt primarily in darkness using smell. Cats are mainly seen near the margins of scrub and forest but ferrets were often observed in the open near rabbit holes (Chapter 3). Because the hunting strategies of cats are quite different from those employed by ferrets, one would expect that the diets of these two species would be dissimilar. Thus, the first objective of this chapter was to ascertain whether there were any differences between the diets of these two predators.

Males and females of sexually dimorphic species are predicted to have different diets (Gittleman and van Valkenburgh 1997). For example, Brown and Lasiewski (1972) suggested that sexual dimorphism in weasels permits resource partitioning by prey size, which reduces competition between males and females of the same species. Adult males of both cats and ferrets are generally much larger than adult females (Blandford 1987; Fitzgerald 1988); therefore, differences in their diets may also be expected. The second objective was to ascertain whether their were any differences in diet between the age and sex of each species.

Generalist predators utilise a broad range of food and habitats while specialist predators exploit a narrow range of food and habitats (Erlinge 1986). Generalists are able to switch from one prey type to another but many specialists are dependent on only one prey type for their breeding success (Andersson and Erlinge 1977). According to optimal foraging theory, diets should be more specialised at high prey densities. Predators should also specialise when profitable prey types are common, and ignore insufficiently profitable prey-types irrespective of their abundance (Charnov 1976). Thus, if a specialist predator encounters a wide variety of prey when searching for food, it would ignore them until it encounters the preferred prey type (MacArthur and Pianka 1966).

Polecats are viewed as generalist predators in Europe because they eat a wide variety of prey (Lodé 1997); however, depending upon location and habitat, they can also be specialists (Weber 1989c; Roger 1991). Likewise, cats and ferrets in New Zealand have also been described as generalist predators (Fitzgerald 1988; Smith *et al.*, 1995); although, Mills (1994) suggested that cats and ferrets in New Zealand are forced to become specialists because of low prey diversity. This then raises the question: do cats and ferrets in New Zealand have a narrow diet and only eat a small range of food or do they have a broad diet and consume all prey types available? Thus, the third objective of this chapter was to examine whether cats and ferrets in North Canterbury, and New Zealand in general, have narrow or broad diets. Finally, the fourth objective was to compare the differences between the diets of cats in New Zealand with those found on islands and in Australia, and the differences between the diets of ferrets in New Zealand and polecats found in Europe.

4.2 Methods

4.2.1. Study Areas

Cat and ferret diets were studied in three areas in North Canterbury, New Zealand. Omihi (172°55'E, 43°03'S) and Scargill sites (172°57'E, 42°56'S), and the Tiromoana site (172°53'E, 43°05'S) were all part of a larger study looking into the effects of controlling ferrets on levels of *M. bovis* as well as the rate of increase of rabbit populations (Caley *et al.*, 1998). The Omihi area consisted of two separate 500 ha farm blocks, *Cotswold* and *The Rock*; for a full description of these sites refer to Chapter 1. The Scargill Valley site consisted of five farm properties covering 3672 ha, ten km north of Omihi. The Tiromoana

site was composed of two farm properties covering an area of 2596 ha, ten km south of Omihi.

4.2.2. Predator Trapping

a) *Omihi*

i) *Cotswold*

In Year One, 40 wire cage traps (610 x 260 x 245 mm) were used to catch cats and ferrets. In the following year, 60 cage traps were used. Traps were spaced at 150-500 m intervals in locations considered likely to catch the target animals. Trapping was carried out during October and December of 1995, January to April, June, August and October of 1996 and between January and July of 1997. As this site was used for a concurrent capture-recapture study, no predators were removed. Traps were set for six consecutive nights and baited with fresh skinned rabbit meat. The traps were checked early the next day and all cats and ferrets caught were tagged, weighed, and sexed. Juvenile ferrets can be as large as adults in only a few months (Ragg 1997), and so their ages were assessed by the presence or absence of a sagittal crest on their skull, as well as tooth wear. Cats weighing under 1500 g are generally less than 6 months old (Fitzgerald and Karl 1979) and these were classified as juveniles. For further details of the trapping protocol and layout refer to Chapter 3.

ii) The Rock

The same trapping protocol was used on *The Rock* as on *Cotswold,* but only 40 cage traps were set during October and December 1995 and between January to April 1996. After this period, and until July 1997, every predator caught using both cage traps and Victor Soft-Catch® leg-hold traps (size 1½) was removed from the study site and most were killed for Tb necropsies. As a result of insufficient scat data for both cats and ferrets from October 1995 to April 1996, prey analysis was carried out combining scats with faecal pellets collected from the rectal passage. Both faecal pellets and scats expelled as waste are referred to in this chapter as scats. Gut contents were not used in this analysis.

b) *Tiromoana and Scargill*

Cats and ferrets were trapped using Victor Soft-Catch® leg-hold traps (size 1½) baited with skinned fresh rabbit meat. Every predator caught was humanely killed and subjected to a Tb necropsy. Traps were set at 100-200 m intervals and were checked daily. Each trapping

session ran between 5-10 nights. Ten trapping sessions occurred between November 1994 and May 1997. Scat remains from the rectal passage were used for the diet analyses. No gut contents were used.

4.2.3. Scat preparation and identification

All scats were placed in a plastic bag, labelled and frozen for later examination. Each scat was assumed to be an independent sample. However, scats from the same ferret captured on consecutive nights and any scats containing only rabbit meat (no fur, teeth or claws) were omitted from the data. Although it may have been possible to weigh cat scats for a quantitative analysis this was not done because of the problems of collecting fresh ferret scats. Unfortunately, many fresh ferret scats stuck to the wire cages and could not be completely bagged and those that were collected were often contaminated by environmental debris which could have biased the data.

Scats were thawed and soaked overnight in disinfectant, before being macroscopically sorted into prey items. After the initial sorting procedure, all scats were then washed through a 250 μm sieve. In most cases prey could be identified after sifting, but some prey items had to be examined under a microscope. Scat remains were divided into nine ecologically relevant prey classes: adult lagomorph, young lagomorph, bird, lizard, invertebrate, rodent, hedgehog, carrion and unidentifiable. Prey identification was facilitated by the use of a predator diet reference collection. Carrion was classified as any prey complete with maggots (dipteran larvae) or identified from a carcass of an animal unlikely to be killed by a ferret, such as a sheep. Lagomorph remains were classified as either adult or juvenile lagomorph (under 500 g) by examining the deciduous teeth, claw length, tails and fur on the skin (see Pierce 1987).

Hare and rabbit hairs are virtually indistinguishable from one another (Day 1966; Brunner 1974). To assess whether rabbit hairs were the same or different to those of hares, a scanning electron microscope (SEM) was used to view their profiles. The SEM photographs revealed few external differences between hare and rabbit hair (Figure 4.1). As a result, all hare and rabbit hair was classified as lagomorph.

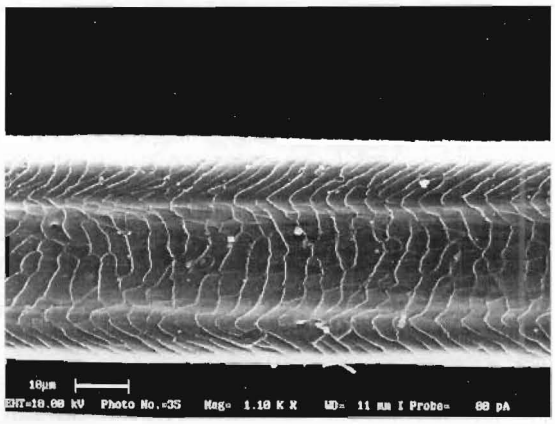


Figure 4.1a. Rabbit (tip).

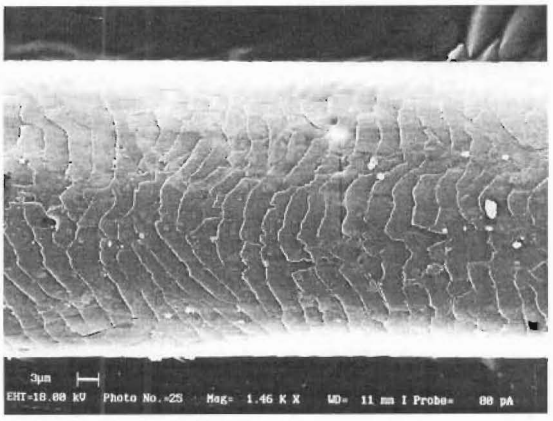


Figure 4.1b. Rabbit (shaft).

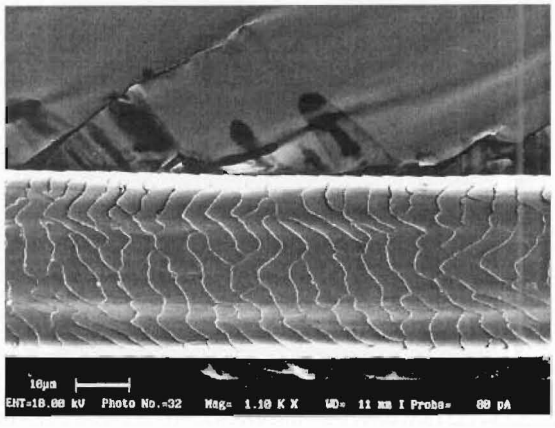


Figure 4.1c. Hare (tip).

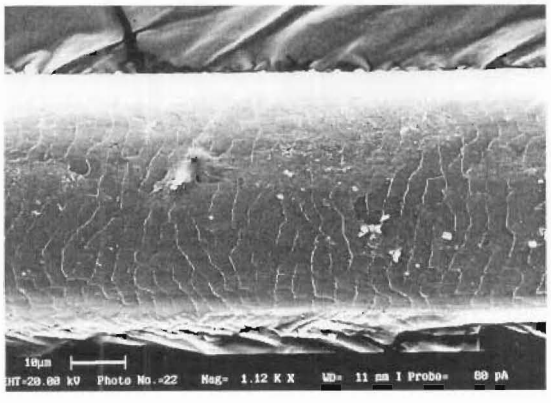


Figure 4.1d. Hare (shaft).

Figure 4.1(a-d). SEM profiles viewing the shaft and tip region of a belly hair from a rabbit and a hare.

Identification of some species was made easier by the presence of certain anatomical features, such as the feathers, beaks, hollow bones, wrinkled skin and claws of birds, the spines and matted coarse hair of hedgehogs, the whole feet and scales of skinks, and the granular reptile skin of geckos. Mouse bones were frequently associated with small tufts of hair while possum hairs were fine and curly with a long shaft region. Often loose ferret and cat hairs without any skin attached would appear in a scat but these were considered as a result of grooming rather than cannibalistic behaviour.

4.2.4. Scat analysis

All results are presented as a frequency of occurrence. This was calculated as the number of occurrences of each prey type divided by the number of faecal samples containing prey, and expressed as a percentage of the monthly and total sample (i.e., it compares the number of times a certain prey occurs with the number of scats containing any prey). When the percentage of each prey group was added together the sum frequency of all prey groups combined sometimes exceeds 100% because many scats contained more than one prey type.

Several disadvantages arise from using a frequency of occurrence methodology. Small prey items may be overestimated if the size of the prey is not taken into consideration, and a scat may contain two meals of the same prey item but are mistakenly counted only once. In addition, the feathers of birds have been observed to have a differential rate of passage through a gut than bones, with feathers generally taking longer than bones (Roser and Lavers 1976). On the other hand, if a large enough sample is collected then using frequency of occurrence is justified in carnivore diet studies (Corbett 1989). Moreover, because it is the most widely used method to estimate cat and ferret diet in New Zealand, it is extremely useful for comparison with previous cat and ferret diet studies.

As scat samples were collected from three independent sites they were initially analysed separately for any inter-site differences. Variation between sites was minimal so the data were pooled to provide one large sample for North Canterbury. In all analyses, sub-adult predators have been classed as juveniles. Because some prey types were too small to test individually for differences between age and sex groups, the prey items were grouped into three categories: 1) all lagomorphs, 2) non-lagomorph vertebrates (birds, rodents, hedgehogs and lizards) and, 3) invertebrates. Chi-square tests were used to test for

significant differences in diet between age, sex and season. To assess seasonal prey variation, scats collected during each season were analysed separately.

4.2.5. Prey Niche Breadth Index

A prey niche breadth index (B = PNBI) was calculated to measure the diversity of both cat and ferret diet using the formula from (Simpson 1949):

$$B = 1/\Sigma\pi_i^2$$

where π_i is the proportion of the diet for the ith prey. Predators with low PNBI values have narrow diets and values of B substantially greater than one indicate predators with broad diets. For example, if predators only consume lagomorphs then $B = 1/1^2 = 1$. (i.e., they have very little diversity in their diet). To investigate whether cats and ferrets in North Canterbury have narrow or broad diets, I compared my results with six other cat studies from mainland New Zealand, six studies from islands, as well as six studies from mainland Australia. I also compared my results against six New Zealand ferret studies and seven polecat studies from Europe. All studies selected for comparison, analysed the diet using the frequency of occurrence method. All but one study, Herekopare Island (Fitzgerald and Veitch 1985), collected diet data over two or more seasons.

4.2.6. Species abundance

No formal prey species abundance indices were measured, except for spotlight counts on rabbits and hares (see Chapter 1). The presence and availability of most prey species could only be obtained from recording non-target species caught in traps set for predators. All non-target species caught were recorded and released, except for stoats on Scargill and Tiromoana and possums on *The Rock* which were killed. No statistical analyses were carried out on these data as they was used only to indicate prey availability. A list of vertebrate prey species encountered at Omihi are presented in Chapter1.

4.3. Results

4.3.1. Cat and Ferret Diet

In total, 260 cat and 478 ferret scats were collected from all three North Canterbury sites. Of these, 242 cat and 305 ferret scats contained identifiable prey items; the balance either contained rabbit bait or had no food remains. Many scats contained more than one prey item with 327 and 373 prey items found in cat and ferret scats, respectively. One cat scat and six ferret scats had prey items that could not be identified.

Lagomorphs were the main prey species eaten irrespective of age, sex and species of predator, occurring in 81% of cat scats and 86% of ferret scats; invertebrates were the second most abundant prey group; followed by reptiles and birds for cats and carrion for ferrets (Figure 4.2).

Seasonally, prey consumption of lagomorphs, non-lagomorphs and invertebrates were similar; however, ferrets consumed proportionately more juvenile lagomorphs in summer and autumn and slightly more adult lagomorphs in spring (Figure 4.3).

No significant difference in diet was found between adult and juvenile cats (χ^2 = 0.01, d.f. = 1, p = 0.90: Figure 4.4a). However, differences were found between adult and juvenile ferrets, with adult ferrets consuming more invertebrates (χ^2 = 4.5, d.f. = 1, p = 0.03) than juveniles and juveniles consuming more birds (χ^2 = 5.2, d.f. = 1, p = 0.02) than adults (Figure 4.4b). Although no difference was found between the diet of female and male ferrets (χ^2 = 0.46, d.f. = 1, p = 0.49: Figure 4.5b), female cats consumed more birds (χ^2 = 7.2, d.f. = 1, p = 0.01), and reptiles (χ^2 = 5.4, d.f. = 1, p = 0.02) than male cats (Figure 4.5a).

When the diet was analysed for differences between age and sex for the three main prey groups (lagomorph, non-lagomorph and invertebrates), the only group that differed significantly were female cats which ate more non-lagomorph prey than males (χ^2 = 17.1, d.f. = 1, p = 0.0001).

4.3.2. Comparison with other studies

In North Canterbury, cats consumed proportionately more rodents, birds, reptiles and invertebrates than ferrets and this was consistent with other studies reported in New

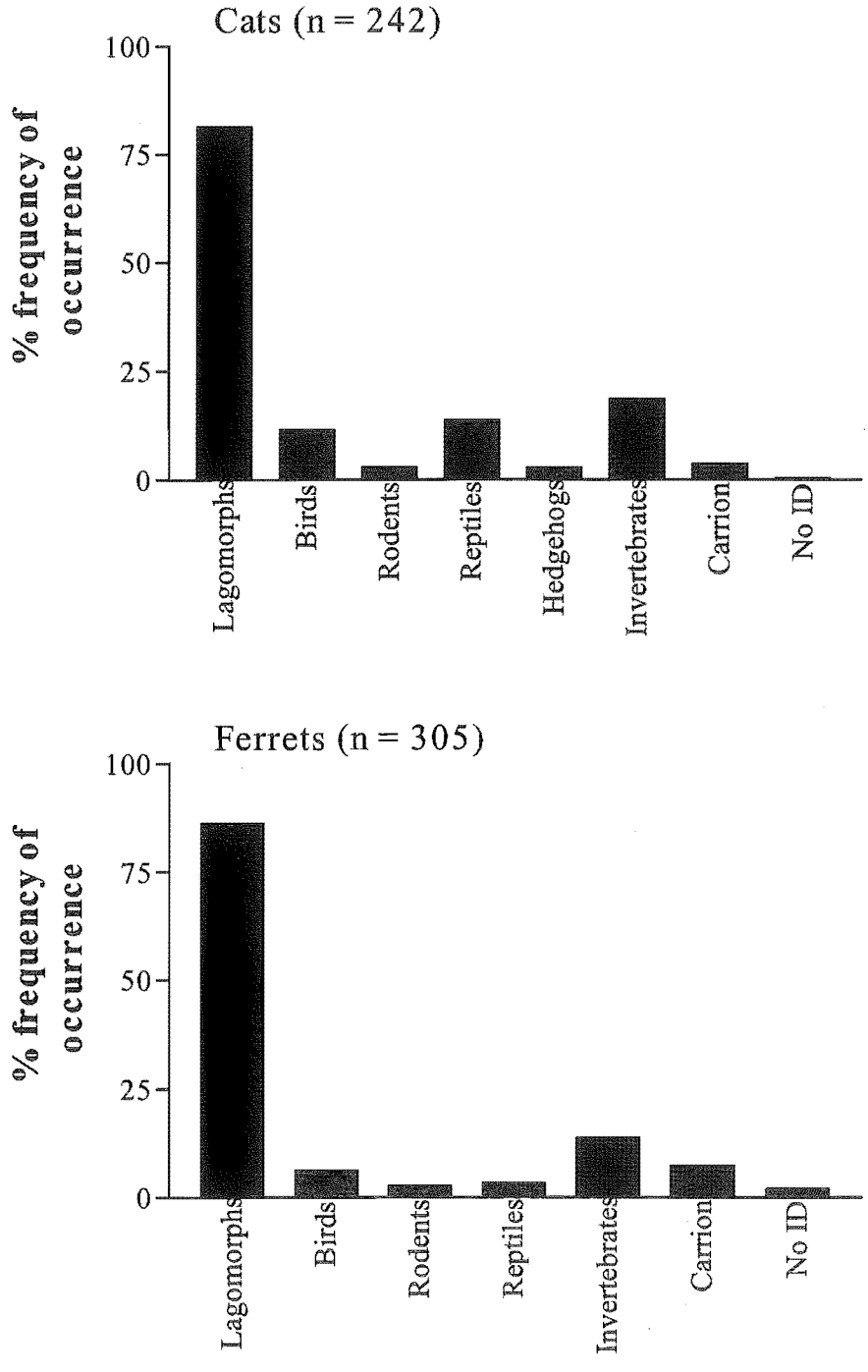


Figure 4.2. Diet of cats and ferrets expressed as percentage frequency of occurrence

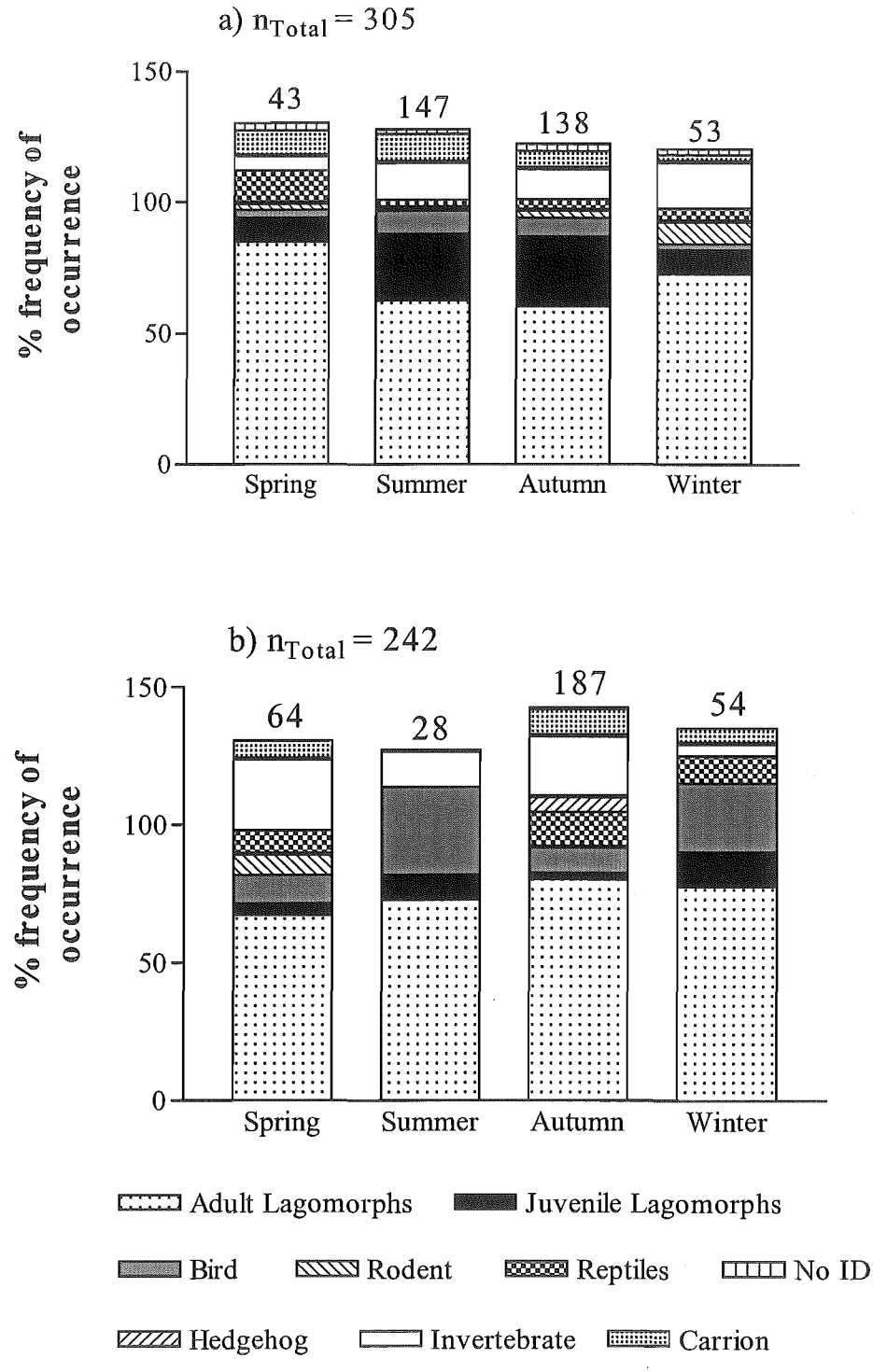


Figure 4.3. Seasonal comparison of the percentage frequency of occurrence of prey groups for a) ferrets and b) cats. n_{Total} = number of scats examined. The numbers above the bars indicate the number of prey items in each prey group.

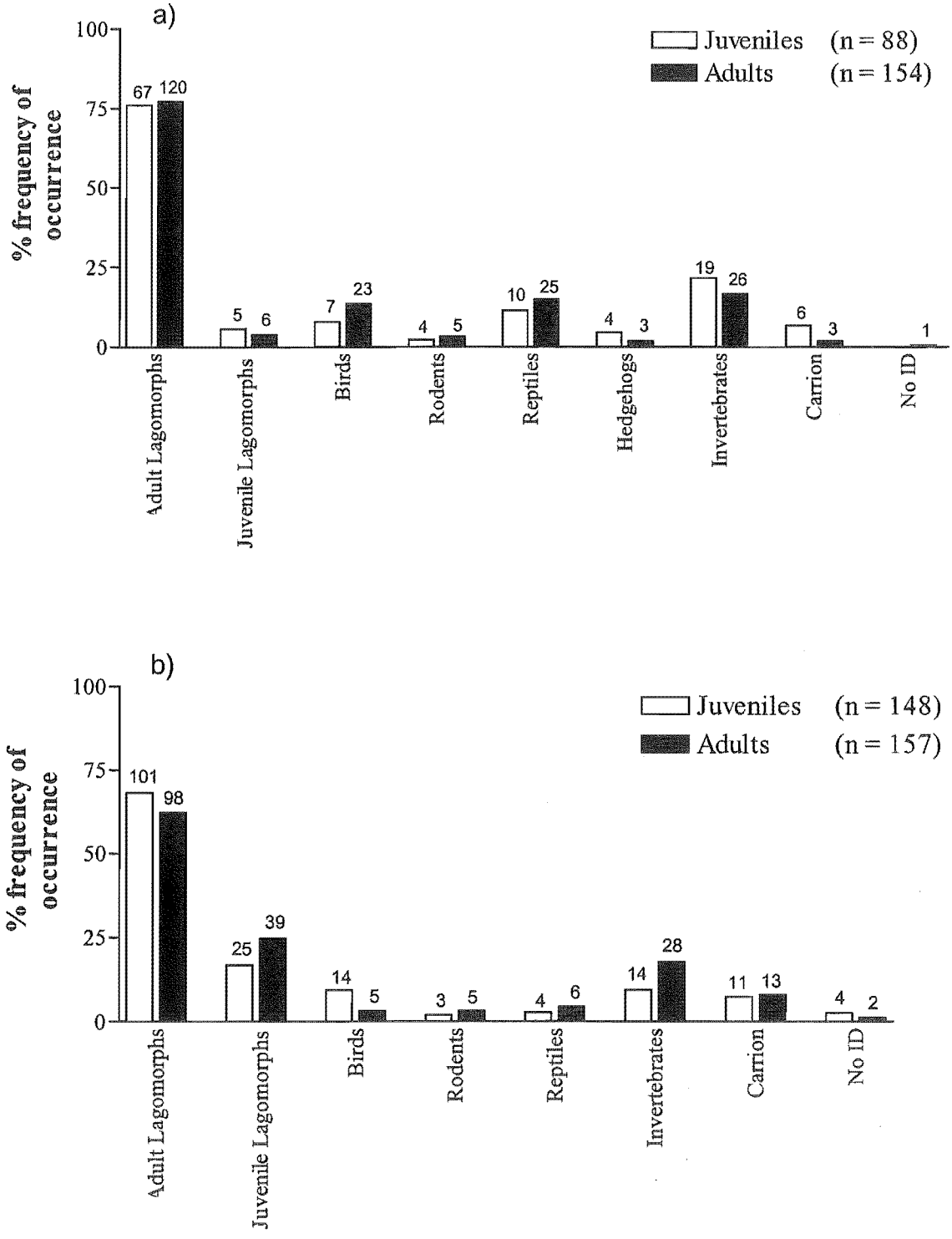


Figure 4.4. Diet of a) cats and b) ferrets for juveniles and adults expressed as the percentage frequency of occurrence of prey items. n = number of scats examined. The numbers above the bars indicate the number of prey items found. **Note:** data for juveniles is only relevant to when they were present

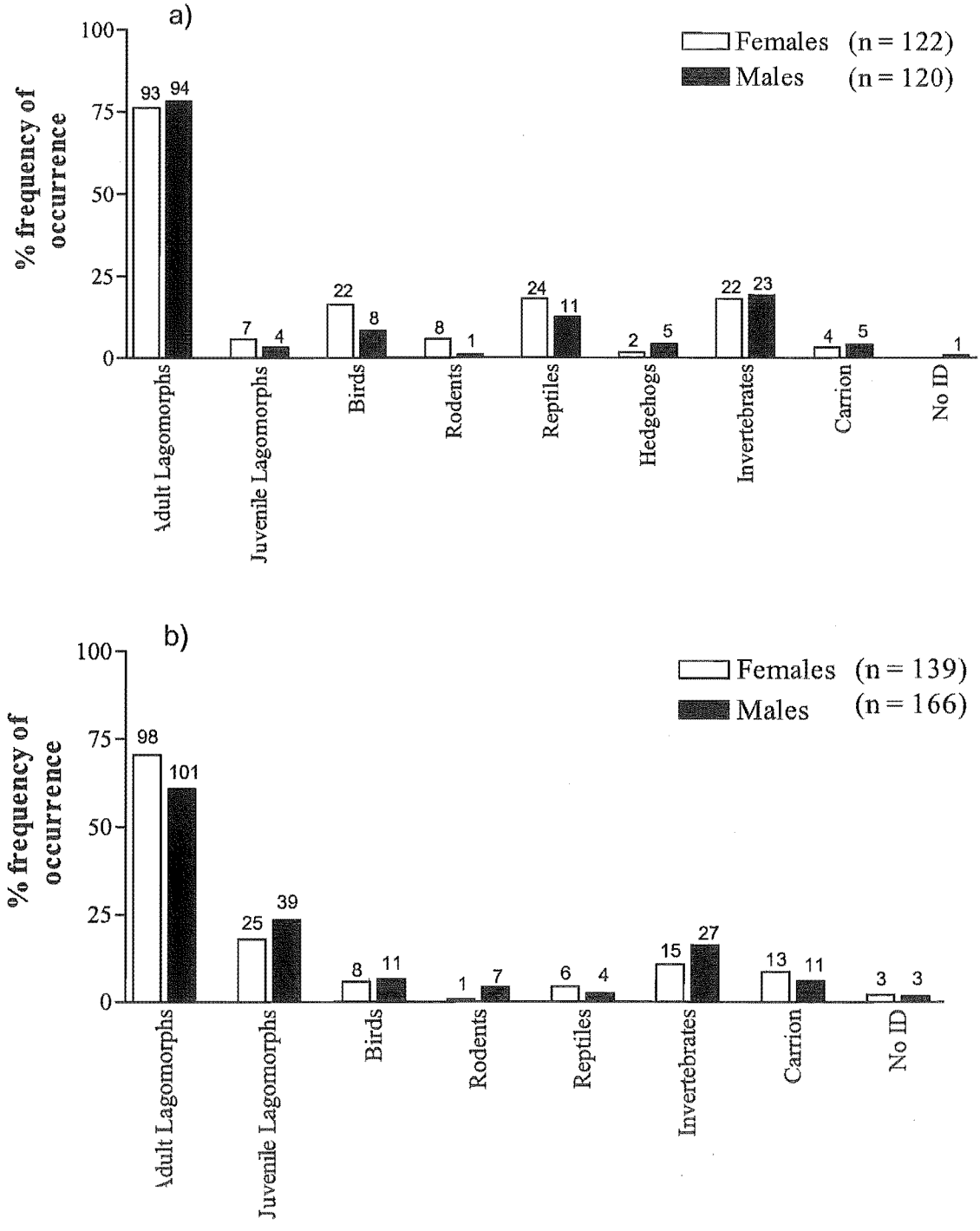


Figure 4.5. Diet of a) cats and b) ferrets for males and females expressed as the percentage frequency of occurrence of prey items. n = number of scats examined. The numbers above the bars indicate the number of prey items found.

Zealand (Table 4.1). In studies where lagomorph consumption was low, particularly on islands, cats mainly ate rodents, birds and invertebrates. However, when lagomorphs were present, such as on the mainland of Australia and New Zealand, cats consumed substantially more lagomorphs than rodents, birds and invertebrates (Table 4.1). Cats in Australia also ate a greater range of other mammals at some sites (e.g., the Eastern Highlands), showing that other mammals were preferred over any other prey group.

In New Zealand, ferrets were six times more likely to consume lagomorphs than birds and fourteen times more likely to consume lagomorphs than rodents (Table 4.2). Although lagomorph was by far the main prey species of ferrets in New Zealand, it was not always the main prey species consumed in each area. For example, in the Manawatu, there was a greater variety of non-lagomorph species consumed (Table 4.2). Relatively, polecats in Europe ate more reptiles and rodents than lagomorphs, however, one study in Southern France showed similar high proportions of lagomorph in the diet of polecats to that observed by ferrets in North Canterbury (Table 4.2).

The lowest PNBI values were ones where only one or two main prey types were eaten, for example, ferrets in Otago, Wairarapa, and polecats in Southern France and Poland (Table 4.2). The highest PNBI values were ones where predators consistently ate high proportions of most prey types, for example, ferrets in the Manawatu and cats in Australia (Table 4.1 and 4.2). The PNBI values indicate that cats on islands generally have the narrowest diets, followed by cats in New Zealand and then cats in Australia (Table 4.1).

The larger PNBI values for cats in Australia probably resulted from the increased amount of other mammals eaten. The PNBI values for cats and ferrets in North Canterbury were 2.48 and 2.06, respectively. Overall, the PNBI values for ferrets and polecats were generally lower than those of cats, which suggests that cats have broader diets than ferrets.

4.3.3. Prey abundance

Effect of lagomorph increase on the diet of cats and ferrets

Lagomorph numbers increased slowly during the first year at Omihi but dramatically increased in the second year after October 1996 (see Chapter 1). Lagomorphs also increased on Tiromoana after spring 1996 (Caley *et al.*, 1998). However, because the

Table 4.1. Diet of feral cats expressed as percentage of occurrence for 7 New Zealand, 6 Island and 4 Australian studies. Mean given for the niche breadth includes ± 1 SE.

	Prey Types									
Location	Lago-morphs	Rodents	Other mammals	Birds	Reptiles	Inverte-brates	Fish	Carrion	n (scats) * = guts	Niche breath
New Zealand										
North Canterbury[1]	81	3	3	12	13	19	0	4**	242	2.48
MacKenzie Basin[2]	86	3	1	6	13	19	0	1	358	2.09
Otago/Canterbury[3]	94-100	14	2	2.3	57	43	0	0	51	3.15
Otago[4]	76	27	17	34	2	23	0	2	62*	3.86
Orongorongo Valley[5]	22	93	19	12	0	57	3	0	677	3.29
Hawkes Bay[6]	1	70	0	31	0	26	0	8**	361	2.78
Wairarapa[7]	68	32	3	59	4	10	0	3	68	3.46
Mean	62	35	6	22	13	28	1	2		3.01 ± 0.23
Islands										
Stewart Island[8]	0	93	5.2	44.1	24	26.2	0	0	229	3.12
Great Barrier Island[9]	0	39	0	71	0	17	0	0	94	2.35
Raoul Island[10]	0	88	4	35	0	58	0	4	57*	2.89
Campbell Island[11]	0	95	0	35	0	60	0	0	20	2.61
Herekopare Island[12]	0	0	0	93	0	47	0	0	30*	1.81
Christmas Island[13]	0	72	10	28	31	62	0	20	93	4.41
Mean	0	65	3	51	9	45	0	4		2.86 ± 0.36
Australia										
North-west Victoria[14]	68	33	7	18	15	44	2	8	131	4.57
New South Wales[15]	48	19	24	45	28	69	19	5	65	5.90
New South Wales[16]	54	9	12	21	30	43	0	4	29*	4.67
New South Wales[17]	82	9	5	4	3	42	0	22	499	3.06
Eastern Highlands[18]	39	3	83	29	3	16	0	3	117	3.25
Western Australia[19]	66	28	2	19	14	39	0	4**	109	4.06
Mean	59	17	22	23	16	42	4	7		4.29 ± 0.52

References: 1) Morley (this study), 2) (Pierce 1987), 3) (Heyward and Norbury 1997), 4) (Alterio 1994), 5) (Fitzgerald and Karl 1979), 6) (Langham 1990), 7) (Gibb *et al.*, 1969), 8) (Karl and Best 1982), 9) (Marshall 1961), 10) (Fitzgerald *et al.*, 1991), 11) (Dilks 1979), 12) (Fitzgerald and Veitch 1985), 13) (Tidemann *et al.*, 1994), 14-15) (Jones and Coman 1981), 16) (Catling 1988), 17) (Molsher *et al.*, 1999), 18) Jones and Coman (1981), and 19) (Risbey *et al.*, 1999). ** if sheep and possum were present in the diet they were analysed as carrion.

Table 4.2. Diet of feral ferrets (*Mustela furo*) expressed as percentage of occurrence for seven New Zealand studies and for seven European studies on the diet of polecats (*Mustela putorius*). Mean given for the niche breadth includes the standard error.

	Prey Types									
Location	Lago-morphs	Rodents	Other mammals	Birds	Reptiles	Inverte-brates	Fish	Carrion	n (scats)	Niche breath
New Zealand										
North Canterbury[1]	86	3	7	6	3	14	0	5*	305	2.06
MacKenzie Basin[2]	74	1	2	2	16	17	0	0	635	2.07
Otago/Canterbury[3]	81	3	4	7	20	32	0	3	123	2.79
Otago[4]	65	4	9	13	4	14	0	2	140	2.61
Otago[5]	87	2	6	12	3	11	0	0	904	1.90
Manawatu[6]	13	19	23	34	17	10	13	11*	223	6.42
Wairarapa[7]	85	1	2	7	0	16	0	9*	85	1.94
Mean	70	5	8	12	9	16	2	4		2.83 ± 0.61
Europe										
Britain[8]	37	32	0	19	6	0	0	5	558	3.55
Russia[9]	0	47	6	3	27	0	0	18	68	3.09
Netherlands[10]	30	25	6	20	20	0	0	0	41	4.29
Southern France[11]	84	9	0	5	0	0	0	3	438	1.39
Switzerland[12]	0	24	0	4	49	3	0	20	285	2.92
Poland[13]	0	16	5	2	74	0	3	1	222	1.75
Belarus[14]	0	34	0	7	40	6	0	13	43	3.32
Mean	22	27	2	9	31	1	1	9		2.90 ± 0.38

References: 1) Morley (this study), 2) (Pierce 1987), 3) (Mills 1994), 4) (Smith *et al.*, 1995), 5) (Ragg 1998), 6) (Roser and Lavers 1976), 7) (Fitzgerald 1964), 8) (Blandford 1987), 9) (Danilov and Rusakov 1969), 10) (Brugge 1977), 11) (Roger 1991), 12) (Weber 1989a), 13) (Jedrzejewski *et al.*, 1993) and 14) (Sidorovich and Pikulik 1997). * if sheep and possum were present in the diet they were analysed as carrion.

counts were completed using a different method to that at Omihi it is difficult to state that the increase observed was in the same order of magnitude. Nevertheless, the rate of increase was similar to that observed for Omihi.

The proportion of cat and ferret scats containing lagomorph was remarkably similar throughout the study, although there were some seasonal differences in the proportion of juvenile and adult lagomorphs consumed (see above). From October 1995 to September 1996, 79% of cat scats and 85% of ferret scats contained lagomorph, while from October 1996 to July 1997, 83% of cats scats and 87% of ferrets scats contained lagomorph. Thus, the large increase in lagomorphs on Tiromoana and Omihi did not affect the proportion of lagomorph found in the scats of cats and ferrets.

Non-target Vertebrates

The number of non-target vertebrate species captured for all three sites is provided in Table 4.3. Hedgehogs were the most numerous non-target animal caught, especially during the spring and summer but they rarely appeared in the diet of cats (n = 7) and never in the diet of ferrets. Most rodents captured were rats as mice were generally too small to be captured in the leg-hold traps and cage traps. Although several birds were captured in the cage traps during spring, most birds appeared in the diet of both cats and ferrets in summer, autumn and winter. All birds eaten were passerines, mainly blackbirds, song thrushes, one fantail and one silvereye (n = 45: cats and ferrets combined).

Possums were abundant on all three sites but they never appeared as a sole prey item in the diet of either cats or ferrets. That is, no possum bones, teeth, claws or clumps of hair with muscle were found without dipteran larvae (fly maggots). However, three cat and five ferret scats contained some possum remains but these were always associated with large dipteran larvae. Sheep were also found in scats classified as carrion (n = 4) and one scat contained two docking rings from the tails of young lambs.

Juvenile rabbits were occasionally captured in leg-hold traps when placed down rabbit burrows but no rabbits were ever captured in cage traps at Omihi. Most young lagomorphs were captured in spring and summer.

Table 4.3. Non-target species trapped from November 1995 to May 1997 on all three North Canterbury sites (Omihi, Scargill Valley and Tiromoana). **Note:** all animals were released alive except for stoats and possums which were humanely killed.

	Spring	Summer	Autumn	Winter	Totals
Stoats (*Mustela erminea*)	37	35	41	21	134
Possums (*Trichosurus vulpecula*)	266	92	154	189	701
Hedgehogs (*Erinaceus europaeus*)	543	558	358	5	1464
Rodents (*Rattus norvegicus, R. rattus* & *Mus musculus*)	33	36	27	25	121
Harriers (*Circus approximans*).	63	34	25	18	140
Magpies (*Gymnorhina tibicen hypoleuca*)	76	19	23	15	133
Birds (*Turdus hilomelos* & *T. merula*)	90	12	10	7	119
Others (i.e., *Oryctolagus cuniculus* & *Lepus europaeus*)	98	64	17	12	191
Total	1206	850	655	292	3003

4.4. Discussion

4.4.1. Diet of cats and ferrets

Few species considered to be major *M. bovis* hosts were found in the diet of either cats or ferrets, although possum remains were found in the scats of three cats and five ferrets. Scat analysis revealed that lagomorph was by far the most common prey species eaten by cats and ferrets in North Canterbury. The frequency of lagomorph in cat and ferret diets was at least four times that of any other prey types. This dominance is consistent with most other New Zealand cat and ferret diet studies (see Tables 4.1 and 4.2); however, the predominance of one prey species over all others in the diet of cats and ferrets is not exclusive to mainland New Zealand. In Europe, lagomorphs were often the most important prey item in the diet of cats (see Fitzgerald 1988) and Roger (1991), found that lagomorphs were the single most important prey of polecats in Southern France, while Jedrzejewski *et al.* (1993) found that anurans were the most important prey for polecats in Poland. Dilks (1979) found that rodents were the most important prey of cats on Campbell Island and, Fitzgerald and Veitch (1985) found that birds were the important prey of cats on Herekopare Island. However, the variety of prey on the islands was very limited.

Dominance by a single vertebrate prey species is not always observed for cats and ferrets. For example, Roger (1991), found that polecats in Central France often consumed two types of prey in almost equal proportion. Similarly, in Britain, Russia, The Netherlands and Switzerland, polecat diet often consisted of two or more vertebrate prey types exceeding 20% of their diet (see Table 4.2). In New Zealand, cats in Hawke's Bay, ate significantly more rodents and birds than lagomorphs (Langham 1990), while ferrets in the Manawatu ate more birds, rodents, reptiles and other mammals than lagomorphs (Roser and Lavers 1976). However, having two or more dominant vertebrate prey species in the diet of cats and ferrets in New Zealand is rare (see Tables 4.1 and 4.2).

In addition to the almost total dominance of lagomorphs, the diet of cats and ferrets in North Canterbury were remarkably similar. They virtually ate the same prey and in almost the same proportion, although a higher proportion of juvenile lagomorphs were consumed by ferrets than cats. Therefore, my hypothesis that the diet of ferrets and cats would be dissimilar, because they use different hunting strategies to capture their prey, is clearly rejected. Possible explanations for the similarity in diet include: a) both predators

have the same optimal diet (prey preference) and, therefore, ignore some prey species; b) low diversity of prey; or c) they were not encountering all prey equally.

Although no accurate prey abundance estimates were collected (other than for lagomorphs at Omihi), the number of non-target species incidentally trapped gives a good indication of what prey types might be available for predators. Much of North Canterbury is pastoral farmland and there are many patches of diverse habitat where a variety of non-lagomorph prey species live. Yet, despite this, only a few species were found in the scats of cats and ferrets. The data collected indicated that some species, such as eels (*Anguilla* spp.), river bullies (*Gobiomorphus cotidianus*), many passerine and non-passerine birds, and frogs (*Litoria raniformis*), were not consumed at all. Even though introduced frogs were often heard in and around the ponds on the farms, they never appeared in cat and ferret scats. Nevertheless, in Europe, frogs were the primary species consumed in several polecat studies (Weber 1989b; Sidorovich and Pikulik 1997). Although better camouflaged than rodents, frogs were possibly targeted because they were easier to seize (Weber 1989c). In contrast, eels (labelled as fish in Tables 4.1 and 4.2) were eaten by ferrets at Pukepuke Lagoon in the Manawatu. No eels were consumed in North Canterbury, even though many eels were observed in the nearby Motunau River at night (*pers. obs.*). Hence, it appears that cats and ferrets were ignoring some species in preference to others.

Some species, such as hedgehogs, stoats, possums, harriers and magpies, may be too large or too difficult for cats or ferrets to capture. Other species, such as house sparrows, may be killed but are relatively unpalatable and appear only infrequently in scats (Fitzgerald 1964). No hedgehogs were found in the diet of ferrets, yet they represented the most abundant non-target prey species captured. The presence of adult hedgehog quills in the diet of cats is thought to be from hedgehogs that were scavenged rather than those killed as live prey. Live hedgehogs are well protected against most predators, therefore, it is not surprising that the only hedgehog remains found in the diet of ferrets at Pukepuke lagoon were juveniles (Roser and Lavers 1976). Possum remains were never found as a single prey item but were found along with large dipteran larvae; thus, they were thought to be a result of the predators scavenging possum. Therefore, species such as house sparrows, hedgehogs and possums, are best considered as opportunistic prey.

Because sexually dimorphic species are predicted to have different diets, many diet studies have separated data by the age and sex of predators (Gittleman and van Valkenburgh 1997). However, several diet studies found no significant differences between

the age and sex of cats and ferrets (Pierce 1987; Fitzgerald 1988; Fitzgerald *et al.,* 1991; Mills 1994; Tidemann *et al.,* 1994; Smith *et al.,* 1995). Similarly in North Canterbury, no substantial dietary differences were found between the sexes of ferrets and between adult and juvenile cats. However, female cats ate more non-lagomorph vertebrate prey (birds and reptiles) than males, adult ferrets ate more invertebrates than juveniles, and juvenile ferrets consumed more birds than adults. A study of ferrets in Otago also found that females ate more non-lagomorph vertebrate prey than males (Ragg 1998).

Seasonally, the proportion of all prey groups consumed did not vary greatly for either cats or ferrets, although ferrets did consume a proportionately more lagomorphs in spring than cats. Most juvenile lagomorphs were consumed in summer and autumn rather than in spring when they are easy to catch in their nests. Although the overall consumption of lagomorph was relatively constant throughout the year, whenever juvenile lagomorphs were present, the proportion of adult lagomorphs in the diet was lower, especially for ferrets. Therefore, when in season, juvenile lagomorphs were the preferred prey.

Although invertebrates are frequently eaten by both cats and ferrets, their contribution to the diet by weight is generally insignificant (Langham 1990; Smith *et al.,* 1995). Indeed, some prey species, when measured by weight, are shown to be much more important than others in terms of their biomass contribution to a predator's diet (Putman 1984). In contrast, by using a percentage frequency of occurrence method, vertebrate species such as rodents and reptiles are often underestimated compared to their contribution to the predators diet by weight. However, invertebrates, by the mere fact that there are many of them, are often overestimated (Reynolds and Aebischer 1991). Therefore, it is important to note that although the percentage frequency of occurrence may be low for rodents and reptiles, in terms of their biomass, their contribution towards a predator's energy intake may be significant (Corbett 1989).

4.4.2. Narrow versus broad diet

Individual PNBI values are useful in quantifying the degree of prey diversity of a predator. Some studies found extremely narrow PNBI values (e.g., ferrets in Otago and Wairarapa and polecats in Southern France and Poland) while in other studies predators had extremely diverse diets (e.g., ferrets in the Manawatu and cats in Australia). Absolute prey specialisation is rare among carnivorous mammals, although it has been found that black-footed ferrets eat nothing but prairie dogs (R. Powell, *pers. comm.*). Although PNBI values

are useful in quantifying narrow diets, unfortunately they are unable to discriminate which prey groups contribute the most to the degree of prey specialisation. For example, even though they live in different predator guilds, the PNBI value for polecats in Poland is similar to ferrets in Otago but the composition of their diets are quite different. Therefore, each PNBI value should be evaluated individually along with the composition (percentage frequency of occurrence) of prey in the diet relative to the prey available.

Smith *et al.* (1995) described ferrets as opportunistic and generalist predators, while cats are considered generalists (Fitzgerald 1988). However, the trophic status of cats and ferrets in New Zealand, as indicated by the PNBI and prey composition values in the areas studied, shows they have a narrow diet. Conversely, polecats in Europe tend to have a broad diet (Table 4.2). One possible explanation for this is that cats and ferrets in New Zealand have a narrower range of prey available to them than European predators, which have a much greater variety of small prey species at their disposal (King 1990). In addition, many of the mammalian species introduced into New Zealand are large and may be too difficult to capture, especially by ferrets e.g., possums (*Trichosurus vulpecula*). Thus, cats and ferrets in New Zealand are forced to eat whatever they can capture. They may take secondary prey such as eels and birds when an opportunity presents itself, but given the evidence above, whether they do actively pursue every possible prey species encountered, is a matter for debate.

Differences in habitat are thought to influence diet. In Europe, polecat diet is more diverse than that of ferrets in New Zealand possibly because they mainly live in wooded, marshland areas which have concentrated populations of small rodents and anurans (Weber 1989b; Lodé 1996). In New Zealand, ferrets are generally found in improved pasture habitats which are more ideal for lagomorphs (Gibb and Williams 1994). Furthermore, predators in Europe often have to alternate between prey species during opposite seasons and in different habitats (Jedrzejewski *et al.*, 1993; Lodé 1994), whereas, lagomorphs, in North Canterbury, breed for almost nine months of the year (Bell 1977). As a result of the continuous availability of lagomorphs, cats and ferrets need not switch to alternative prey.

Differences in habitat may also influence prey diversity. The main difference between the diet of cats found on islands, compared to those on mainland New Zealand and Australia, was the diversity of potential prey. Cats on island habitats ate mainly rodents, birds and invertebrates, as very few vertebrates, such as lagomorphs and reptiles, were available. As a consequence, cats found on islands have a narrower diet than cats studied

on mainland New Zealand and Australia (Table 4.1). Although some identical prey species, such as rodents and some species of bird, are found in both habitats (Karl and Best 1982; Fitzgerald and Veitch 1985), when comparing the diet of island predators to mainland predators, those species common to both habitats are consumed in differing proportions. For example, although rodents are found in mainland habitats, mainland predators prefer larger and presumably more profitable species, such as lagomorphs. Therefore, differences in habitat may strongly influence prey selection.

Like New Zealand, lagomorphs were introduced into Australia, but in terms of prey diversity, cats in Australia have a wider range of mammalian prey under 1 kg to choose from. For example, Australia has at least 65 species of bat (Order Chiroptera), 60 species of rodent (Order Rodentia), 16 species in the Order Diprotodonta (possum), 48 species in the Order Dasyuromorphia (dunnarts and dibblers), six species in the Order Permelemorphia (bandicoots and bilbies), and a single mole species (Order Notoryctemorphia) all under 1 kg in weight (Strahan 1995). Nevertheless, even when there is a greater diversity of prey available, cats in Australia, like their New Zealand relatives, still consume lagomorph more than any other prey (Jones and Coman 1981; Molsher *et al.*, 1999). The reasons for this are not clear but would be worth investigating.

Specialist predators normally concentrate in areas where there is an abundance of their preferred prey. By focusing on prey in localised areas, predators can reduce their searching time to forage in a more optimal manner (Andersson 1981). This appears true for ferrets in North Canterbury, as they were mainly found in grassland areas where rabbits thrive. Other diet studies from grassland habitats within New Zealand confirm that cats and ferrets specialise on lagomorphs (Mills 1994; Ragg 1998), but in non-grassland habitats, such as the Orongorongo Valley, Hawke's Bay and Manawatu, they eat a greater diversity of non-lagomorph prey (Gibb and Flux 1973; Roser and Lavers 1976; Langham 1990).

Prey specialisation frequently occurs when preferable prey are common and when prey density is high; however, this does not always mean that predators are able to regulate prey numbers (Sinclair and Pech 1996). Although rabbit numbers increased substantially after October 1996 on both *The Rock* (where predators were being removed) and on *Cotswold* (the control site) by several orders of magnitude, no significant difference was observed in the rate of increase between the two sites. However, an increase in hares was observed, with *Cotswold* having more hares than *The Rock*. Nevertheless, the proportion of lagomorphs in the diet of both cats and ferrets remained unchanged. This suggests that the

gut capacities of cats and ferrets were already near their satiation level before rabbit numbers dramatically increased. Thus, the predators were unable to maintain the lagomorph population at an equilibrium level. Interestingly, lagomorph numbers on *The Rock* had been relatively low and stable for almost twenty years prior to this dramatic increase (Bell 1990), and predation had been considered the major limiting factor (Robson 1993). It is possible that once lagomorph numbers got beyond a certain threshold, predation by ferrets and cats ceased regulating the lagomorphs.

Regulation of prey is possible when predators have a direct density-dependent effect over low density prey (Sinclair *et al.,* 1990). A study in Australia that removed predators from one site while retaining those in another site, found that rabbit populations were regulated by predators if their density was kept low; nevertheless, if the population increased beyond a certain threshold, the prey would escape regulation (Pech *et al.,* 1992). With the large increase in lagomorphs in North Canterbury after September 1996, there was a corresponding increase in predator populations (see Chapter 3); however, even with the new recruits, the predators could not regulate lagomorph numbers. That is, they could not return the lagomorph population, through density dependent factors, back to its original equilibrium.

In summary, lagomorphs are the staple prey of cats and ferrets in North Canterbury. Other than the higher proportion of juvenile lagomorphs consumed by ferrets taken from burrows, cats generally ate the same prey, in almost the same proportion, as ferrets. Prey availability and prey preference are considered the main reasons for the matching dietary patterns despite differences in predator hunting behaviour. Similar diet results, to that seen in North Canterbury are also observed for most other cat and ferret studies in New Zealand. The only exceptions are cats and ferrets living in areas where lagomorphs are not abundant. Although cats and ferrets use quite different hunting strategies to capture their prey, the similarity in diet clearly demonstrates the adage that there is often more than one way to catch prey. Finally, ferrets generally have narrower diets than cats, and cats and ferrets in New Zealand generally have narrower diets than cats in Australia and polecats in Europe.

4.4.3. Management Implications

Because cats and ferrets in New Zealand are almost totally reliant on lagomorphs, and because there are only a few alternative prey species available, a reduction in cat and ferret numbers may be possible by reducing lagomorph numbers. Indeed, research by Norbury and McGlinchy (1996) and Norbury *et al.,* (1998) concluded that reductions in cat and ferret numbers are likely after major rabbit control programmes but, they also found signs of prey switching. Nevertheless, even when rabbit numbers were reduced by up to 99%, rabbit still appeared in over half of all predator scats (Heyward and Norbury 1997). The continual presence of lagomorph in the diet, even when prey numbers decline, strongly suggests that cats and ferrets are indeed specialising on their preferred prey (lagomorphs). Therefore, the best strategy to lower cat and ferret numbers may be to continuously reduce lagomorph numbers, and at the same time protect any susceptible native species likely to be impacted should the cats and ferrets switch to other prey. To date, all studies of ferret diet and prey switching have been of relatively short duration. It is clear from my work that a long-term study (> 10 years) is now required to examine; a) the likely impacts of prey switching, either in the interim period after lagomorph control or permanently, to native species, and b) to determine if cats and ferrets continue to remain at a low density once lagomorph abundance is kept low.

Finally, under favourable lagomorph conditions, the increases in lagomorph abundance observed appear to be independent of cat and ferret predation pressure. That is, the cats and ferret were unable to regulate lagomorph numbers once they crossed a certain threshold. From a management perspective, this implies that removing predators, especially ferrets for Tb, when lagomorph survival is favourable will not exacerbate increases in lagomorph numbers.

Chapter Five

Testing the ability of an acoustically sensitive transmitter system to identify small mammal behaviour.

5. Abstract

Studying ferret (*Mustela furo*) behaviour under natural conditions is extremely difficult. Conventional radio tracking is useful to measure an animal's activity patterns but has not been able to measure individual behaviours because differing activities can result in identical signals. This study tested how an acoustically sensitive transmitter system (ASTS) could be used to identify the individual behaviours of an animal from its sounds and vocalisations, in this case a ferret. First, all sounds and vocalisations were calibrated by simultaneously video taping the activities and behaviours of a ferret fitted with an ASTS collar while housed in an observation enclosure. Second, after a library of sounds and behaviours had been documented, the ferret wearing an ASTS collar was released into a much larger semi-natural enclosure and the sounds of its activities and behaviours recorded. ASTS technology has many advantages, such as obtaining a faithful record of an animal's behaviour, documenting rare and unusual behaviours that may occur when an animal is underground or out of sight, as well as recording an animal's vocalisations. However, it also has certain limitations, such as a short battery life, occasional loss of audio signal when out of range or when deep underground, as well as no efficient way of analysing large volumes of data. Nevertheless, ASTS technology is seen as a complementary method to conventional radio tracking and, when used effectively, has the potential to document behaviours of a variety of animals once thought impossible to study in the wild.

5.1 Introduction

Studying an animal's natural behaviour can often be extremely difficult. Ferrets (*Mustela furo*) are no exception. They are naturally shy, elusive and generally regarded as nocturnal (Blandford 1987; Lavers and Clapperton 1990). Moreover, their long slender bodies are low to the ground which can make them difficult to observe even when they are out of their dens (Weber 1989). As a result, the behaviour of wild ferrets under natural conditions has been poorly documented.

One of the greatest advances in ecological research has been the development of radio tracking (Mech 1983; Kenward 1987). Radio tracking has not only provided an excellent tool for locating and monitoring an animal's home range and movements, it has also been used to obtain *in situ* information about their physiology (e.g., heart rate and temperature; Cochran 1980). In addition, radio tracking has been used by researchers to interpret activity patterns over extended periods of time (see Lodé 1995; Doncaster and MacDonald 1997; Drew and Bissonette 1997). To establish the activity pattern of an animal, a commonly used method is to monitor a radio-tagged individual for less than 60 seconds at intervals of 5 minutes or longer. The integrity of a radio signal is then used to predict whether an animal is active or inactive. If a signal varies substantially, the animal is regarded as active; if the signal is constant, the animal is recorded as stationary or resting (Craighead *et al.,* 1973).

Using variations in signal strength, pitch, and pulse rate to describe the behaviour pattern of an animal is potentially subjective and possibly inaccurate for two reasons. Firstly, describing the behaviour of an animal using conventional radio tracking signals may be impossible, as differing activities (e.g., moving and eating) can produce identical signals; as a consequence, the activities of the animal may be incorrectly classified (Greager *et al.,* 1979). Secondly, because radio signals can be reflected or diffracted depending on the animal's position (e.g., its elevation above ground), the strength and/or pitch of the signal may change accordingly (Kenward 1982).

Although an animal may be identified as active, establishing what the animal is actually doing is fundamental to learning about the its natural behaviour, while measuring the length of each behaviour helps in developing time-energy budgets (Jacobsen and Wiggins 1982). Acoustically sensitive transmitter systems (ASTS) can potentially solve the problem of determining what an animal is doing and when it is doing it. An ASTS is

essentially a small microphone, transducer amplifier, modulator and transmitter fitted on a collar. The sounds detected are either vocalisations made by the study animal, or by conspecifics and other animals, or sounds produced from a variety of behavioural activities. An experienced researcher, using an ASTS, can identify with relative ease a variety of behaviours as well as the length of time that each behaviour continues (Greager *et al.,* 1979; Alkon and Cohen 1986). Furthermore, ASTS can provide valuable information on vocalisations, especially with conspecifics, as well as information on behaviours which cannot be directly observed (e.g., when animals are underground or behind an obstacle).

Although ASTS technology is not new, few people have used this remote sensing system as a tool in behavioural research (D. Ward, *pers comm.* Sirtrack Ltd.). A sensing system that can assist with describing what an animal is doing and when it is active, opens up many behavioural research possibilities. The first objective of this chapter was to show how sounds and vocalisations made by a ferret could be identified and associated with certain behaviours. The second objective of this chapter was to report on the effectiveness and reliability of ASTS technology and to discuss some of the benefits and limitations.

5.2 Methods

The methods section is divided into two parts. The first section describes how ferret sounds and vocalisations were calibrated by simultaneously video taping the activities and behaviours of a ferret fitted with an acoustic transmitter, while occupying a small observation enclosure. The second section describes how ferret vocalisations and behavioural sounds were recorded from a ferret fitted with an ASTS collar, while occupying a large semi-natural enclosure at the Templeton Research centre. In both methods, only a single male ferret wearing the audio collar was recorded; however, it was recorded interacting with other collar-less female ferrets placed inside the enclosures.

5.2.1. Observation enclosure

a) ***Calibration of Ferret Vocalisations***

The audio-visual study was conducted in an outdoor observation enclosure located in Christchurch, New Zealand. The enclosure was 3 m wide x 4 m long and 1 m high. Square wire mesh (1 cm x 1 cm) was attached to a wooden frame on each side as well as the floor of the enclosure. A 0.3 m ninety degree inverted overhang was constructed on three sides

of the enclosure while the fourth side had a wide (600 mm) piece of tin running along the wall. Both the wire overhang and tin meant that a roof was not necessary, as ferrets are poor climbers. A sheet of heavy plastic was placed over the overhang to provide shelter from rain.

The enclosure was placed alongside a wall from which a Burle® CCD video camera (8 mm auto iris lens) was mounted 2.3 m above the enclosure. By mounting the camera at this height, 96% of the enclosure could be viewed without any distortion. Two 12 v battery- operated infrared arrays were placed at either end of the enclosure providing infrared light over 95% of the area visible from the CCD camera.

Inside the enclosure, were a range of artificial and natural features. These included a den where the ferret(s) rested, two toilet-trays (full of soil), a concrete drinking bowl, a pile of logs, two small bushes, two plastic tunnels buried under mounds of dirt, with one plastic tunnel on the surface. Each plastic tunnel had a different diameter (55, 75 and 100 mm); the smallest tunnel could be used as a refuge by the female, as the male was too large.

Fresh food, mainly skinned rabbit, was supplied daily. Efforts were made to randomly place food at different times and in different locations within the enclosure to avoid any cyclical rhythm associated with food provision. This was to avoid food provision providing a reason for starting any activity.

b) *Recording Protocol and Methodology*

This section of the study involved two sessions of 96 hours of continuous recordings, one in February and one in March 1997. A further 24 hours of recordings was made during the breeding season to provide information on ferret courtship as well as mating behaviour and vocalisations. In February, a lone male ferret was used, while in both March and October, a male and female pair both occupied the enclosure. For a week prior to any audio recordings, the male was fitted with a dummy collar. No apparent behavioural differences were observed.

Because the study required the audio transmitter to be worn continuously, two concerns were raised. Firstly, the possibility that the weight of the collar would affect the ferret's natural behaviour. With a ½ AA lithium battery, the collar weighed 60g, which is much less than 5% of the average weight of an adult male ferret ($\bar{x}$ = 1500 g), but over the 5% standard if used on an adult female ($\bar{x}$ = 830 g). With a ⅔ AA lithium battery the collar weighed 70 g, marginally less than 5% of a male ferret's weight. The second concern was

the short life expectancy of batteries. With continuous operation, the expected life of a ½ AA and ⅔ AA battery is 10 and 13.5 days, respectively. Prior to recording, both types of battery were tested on a ferret, with no obvious behavioural differences observed with either collar. However, even though the ⅔ AA battery offered a longer operating time, the ½ AA battery was eventually used for these trials because the collars were lighter and the life expectancy sufficient for the study's requirements.

Each audio transmitter was fitted onto a wide cable tie and placed around the ferret's neck 24 hours before a recording session began. The audio transmitting frequency was set at 160.1625 MHz and, instead of the standard brass loop collar commonly used for radio tracking ferrets, a 220 x 1.5 mm stainless steel whip aerial was used to increase audio output and reduce the signal/noise ratio. The microphone (type EA-1934) was immediately activated as soon as a magnetic switch was removed from the transmitter.

The audio signal was picked up via a nearby aerial and relayed to a dual conversion narrow band Salcom® SR160 data receiver. The audio signal was then simultaneously recorded with the CCD video images of the ferret's behaviour onto a Philips® VR6549 video recorder (VCR). All recordings were in real time and, as image and sound quality was critically important, only short play video tapes (3 hour) were used.

c) *Data Management and Analysis*

An all occurrence sampling method was used to provide an exact record of each behaviour/vocalisation and time of occurrence. All VCR tapes were viewed and analysed in real time, as any fast-forwarding created sound loss. Each tape was played through a television monitor while the behaviours and times were summarised onto a prepared check sheet.

With the assistance of the video, virtually every behaviour could be identified. In all, ten behaviours were classified (see Table 5.1). Only when the ferret was out of camera range, or in its den, could video footage not be used to distinguish different behaviours; therefore, all activities out of camera range were omitted from the statistical analyses.

Each behaviour was regarded as mutually exclusive (i.e., a ferret, for recording purposes, could not be recorded as active and moving at the same time). In some instances the ferret would start a behaviour, pause, and then continue with the same behaviour. By allowing a 5 second interval between behaviours, I could determine if the ferret changed its behaviour or started a new behaviour. If the ferret changed its behaviour, then the time

recorded for the new behaviour would be taken from the point where the behaviour first changed.

Ferrets are generally regarded as nocturnal animals (Lavers and Clapperton 1990). Therefore, to test the null hypothesis that a ferret's activities and behaviours were similar over a 24 hour period, all active behaviours were divided into: a) those that occurred during the day (diurnal behaviour) and, b) those that occurred during the night (nocturnal behaviour). The times of sunrise and sunset delimited the diurnal phase; the twilight of dusk and dawn was included in the nocturnal phase from sunset to sunrise (New Zealand Standard Time). In statistical terms, the division of diurnal activity and nocturnal activity may not be truly independent because what the ferret did during the day may affect its night-time activities. For example, if the ferret ate for 10 minutes just before sunset, the probability of the ferret eating for another 10 minutes just after sunset would be affected by its earlier meal.

Because of the large variations in activity times a $\log_{10}$ transformation was used to normalise the data. Fixed factor two-way ANOVAs were used to test the null hypothesis that mean activity times for each behaviour during the day and at night were the same.

The activity rate of the ferret was defined as the number of times the ferret changed from one activity to another activity per hour. To determine if the number of activities observed during daylight hours were similar to those observed at night, G-Tests for contingency table data (log likelihood ratio tests) were used (Zar 1999).

5.2.2. Semi-natural enclosure

The audio study was conducted using a predator-proof enclosure located at Templeton (43° 32" S: 172° 27" E), 14 kilometres south of Christchurch, New Zealand. The enclosure was almost 1 hectare in size (100 x 75 m) and was established by the Department of Scientific and Industrial Research (DSIR) to study rabbit behaviour and biology in the 1970s. At the time of this study, a small remnant population of rabbits (*Oryctolagus cuniculus*) inhabited the enclosure. The rabbits have, over time, established a large network of warrens in the sandy soil and much of the pasture had been grazed so that rabbit paths were easily identified. Built inside the perimeter fence is a shed from which all observations and audio recordings were made.

Table 5.1. Ferret behaviours in the observation enclosure with a description of each behaviour and its associated vocalisations/sounds.

Behaviours	Description of behaviours and associated vocalisations/sounds
Active	Sounds associated with grooming, scratching, vigilance, and moving (but not physically moving from one location to another location).
Active and calling	Same as active but the ferret vocalising. i.e., chattering sounds.
Active outside of camera range	Same as active but outside of CCD camera range (could also be inside the den)
Defecating or urinating	Defecating or urinating and scent marking.
Drinking	Drinking, i.e., lapping and swallowing sounds
Eating	Eating, i.e., masticating and swallowing sounds
Female contact	Sounds associated with female interaction such as mating, courting, playing. i.e., chattering, growling & screaming sounds
Digging	Digging and scraping sounds (normally erratic)
Moving	Moves from one location to another location; e.g. stepping sounds
Sleep/inactive	Sleeping. Whimpering, snoring and breathing sounds. All inside den.

The predator-proof enclosure was constructed of rabbit netting buried 1.5 m into the ground. The height of the fence was 2 m and had a 0.8 m overhang to prevent wild animals entering the enclosure. In addition, a single electric wire (240 volts DC) at the top of the fence ran around the inside perimeter.

a) ***Preliminary tests, recording protocol and methodology***

Preliminary tests were carried out both in the field as well as inside the semi-natural enclosure. The tests were designed to determine the maximum audible listening range of the ASTS as well as the maximum depth underground. The tests used two domesticated ferrets, neither of which was used in the main study.

Because the objective of the study was to ascertain the behavioural activity of a ferret, a focal sampling technique was used. This section of the study involved two sessions of 96 hours of continuous recordings, one in April and one in June 1997. This meant that one individual could be followed for a continuous period of time for each of the trials in April and June. The audio signal was picked up via a 3-element Yagi aerial permanently mounted on the observation shed within the enclosure and relayed to a dual conversion narrow band Salcom® SR160 data receiver. The audio signal was then digitised through a Sony® PCM (pulse code modulator) and recorded onto a Philips® VR6549 long play video recorder (VCR) for later analysis. On the long-play function, a single four hour video tape could record continuously for eight hours.

A male ferret was acclimatised for one week in the enclosure before being trapped and fitted with the ASTS collar. The collar not only had an acoustic transmitter, but also a locator beacon emitting at 20 pulses per minute, allowing the ferret to be tracked to a den.

Two female ferrets, fitted only with locator tracking collars, were released into the enclosure two months before the male ferret so they could acclimatise themselves to the new environment. No tracking collars were put on the female ferrets until the day before the first trial began. In addition to the two females, a second male ferret was housed in a cage inside the enclosure (so as to prevent injury to either male). Each ferret was ear-tagged and weighed when first placed inside the enclosure. All ferrets used were wild-caught animals.

Inside the enclosure eight cage traps were randomly placed and set to capture ferrets before and after each trial. When the traps were not set, 150 grams of rabbit meat or sardines was placed inside some of the traps every second day to provide a supplementary

food source for the ferrets. This also encouraged the ferrets to habitually venture inside the traps.

b) *Data Management and Analysis*

As in Part A, all non-vocal behaviours of the ferret could easily be identified acoustically. Without video information, an initial assumption was made that the ferret's sounds and vocalisations at Templeton were the same as those made in the observation enclosure. However, not all sounds were exactly the same. For example, when the ferret was moving at Templeton, it had a natural environment rather than an artificial one. The natural environment created a wider range of background sounds. Nevertheless, the sounds associated with each type of behaviour were consistent with those heard in the observation enclosure.

To assess the reliability of identifying each sound as well as when they began and finished, all behaviours that could be directly observed were entered onto prepared check sheets and later compared to the acoustic VCR recordings from the same time period. Intra-observer reliability between the direct observations and the acoustic VCR recordings were calculated using a Spearman rank correlation coefficient for 12 pairs of 10 minute intervals. Behaviours directly observed were *active, active and calling, drinking, eating, digging, moving, moving and calling* and *male contact* (see Table 5.2 for the definition of each behaviour). *Female contact, sleeping/ inactive* and *transmission loss* were not directly seen but were identifiable from their distinctive sounds and associated time periods. In addition to the intra-observer reliability tests, known sounds from Templeton were compared visually using spectrum analysis techniques in the bioacoustics programme Canary® to confirm whether the sounds heard at Templeton were the same as those made in the observation enclosure. As in Part A, each behaviour is regarded as mutually exclusive.

Transmission loss, although not a behaviour, was also measured. If the audio signal was intermittent with very short bursts of a particular behaviour the signal was classified according to that behaviour. However, if the signal was lost for more than 15 seconds it was recorded as transmission loss. Transmission loss resulted either when: a) the ferret was deep underground (> 1.5 m); b) when the ferret was active next to the wire fence or in the cage traps; or, c) through some technical difficulty.

All data for Part B of this chapter was analysed using the same procedures as described in Part A.

Table 5.2. Ferret behaviours at Templeton with a description of each behaviour and its associated vocalisations/sounds. **Note**: intermittent periods of transmission loss were occasionally associated with some behaviours. Although originally classified according to the table below these behaviours were combined for all analyses.

Behaviours	Description of behaviours and typical vocalisations/sounds
Active	i) Ferret grooming, scratching, and moving (but not physically moving from one location to another location). ii) Same as active but with short intermittent periods of transmission loss
Active & calling	i) Same as active but the ferret would be vocalising. i.e., chattering sounds. ii) Same active & calling but with short intermittent periods of transmission loss
Drinking	Ferret drinking. i.e., lapping and swallowing sounds
Eating	Ferret eating. i.e., masticating and swallowing sounds
Female contact	i) Interacting with female ferret. i.e., mating, courting, chattering, growling & screaming ii) Same as female contact but with short intermittent periods of transmission loss
Digging	i) Digging, scraping sounds, (normally erratic) ii) Same as digging but the ferret would be vocalising i.e., chattering. iii) Same as digging but with short intermittent periods of transmission loss
Moving	i) Moves from one location to another location (background noises) ii) Same as moving but with short intermittent periods of transmission loss
Moving & calling	i) Same as moving but the ferret would be vocalising, i.e., chattering. ii) Same as moving & calling but with short intermittent periods of transmission loss
Male contact	i) Male ferret in contact with other male ferret, i.e., growling, hissing ii) Male ferret vocalising with other male ferret. Both ferrets chattering
Sleep/inactive	i) Sleeping , i.e., whimpering, snoring and breathing sounds ii) Same as sleeping but with long periods of transmission loss
Transmission loss	Transmission loss (>15 seconds). Indicates the ferret was underground (>1.5 m)

c) ***Recording times for the observation enclosure and Templeton***

A total of 192 hours of recordings were made of the ferret wearing the ASTS collar in the observation enclosure as well as at Templeton. However, only 72 hours of continuous data for February and 72 hours for June (translated as three full days of recordings for each of these months) was used in the analysis. This was done because five and a half hours of recordings at the end of June were exceptionally poor, due battery power loss. Although it was possible to hear some loud activities, some quiet activities may have been missed. Therefore, to obtain some standard between the months, it was decided to use only 72 hours of continuous recordings.

5.3. Results

5.3.1. Activity patterns

In using ASTS technology to examine when a ferret was active and inactive, it was found that the ferret was active on average in the observation enclosure 24% of the time, with activity ranging from 21% during the day to 28% at night. It was found that the ferret in the observation enclosure displayed no singular peak period of activity, with only a weak bimodal activity pattern evident (Figure 5.1a). The ferret was inactive in the observation enclosure for 76% of the time, with the average time for a period of inactivity being 47 minutes during the day and 33 minutes at night. The range of times that the ferret was inactive in the observation enclosure is shown in Figure 5.2a.

Similarly, at Templeton, the ferret was active, on average, 22% of the time, with most activity occurring in the early evening. Daytime activity at Templeton was 16%, while the ferret was active 28% of the time at night. However, Figure 5.1b shows that the ferret had a singular peak period of activity in the early evening from 1700 to 2200 hours with very little activity during the rest of the night (Figure 5.1b). This shows that compared to the observation enclosure, the Templeton ferret displayed no distinctive bimodal activity pattern (Figure 5.1b). In addition, Templeton data showed similar inactive rates to that found in the observation enclosure, with the ferret inactive for 78% of the time. However, the average time for a period of inactivity was approximately 1½ hours during the day and 1 hour at night. The range of times that the ferret was inactive at Templeton is shown in Figure 5.2b.

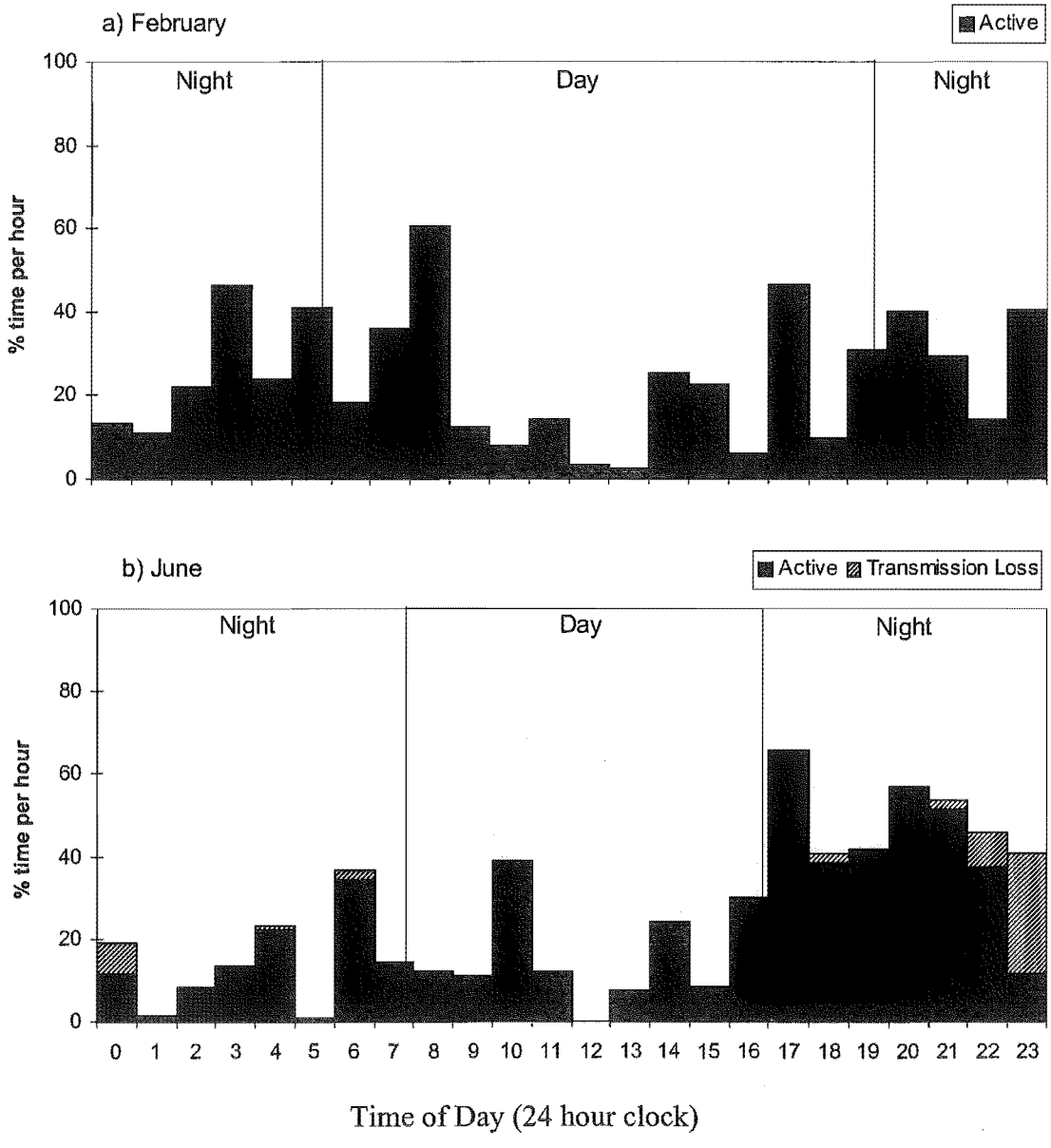


Figure 5.1. Activity budget of the ferret in a) the observation enclosure and, b) at Templeton. (Data averaged from 72 hours of observations).

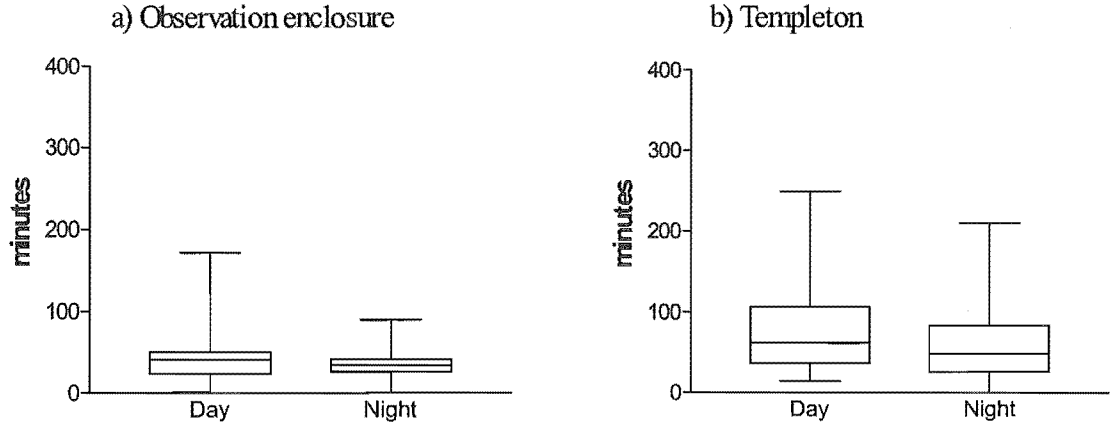


Figure 5.2. Duration of ferret inactivity for a) the observation enclosure and, b) at Templeton. The box extends from the 25th percentile to the 75th percentile, with a horizontal line at the median (50th percentile). Whiskers extend down to the smallest value and up to the largest.

5.3.2. Activity rates and times

ASTS data showed that the frequency of changes in behaviours displayed in the observation enclosure averaged 10.5 activities per hour (Figure 5.3a); however, the number of activities averaged 9 per hour during the day compared to 13 per hour at night. Peak activity rates formed a stronger bimodal pattern with peaks at 0700 and 2300 hours (Figure 5.3a).

Although, at Templeton the frequency of behaviours averaged 7.8 activities per hour (Figure 5.3b), again, the number of activities observed per hour during the day were often different from the number of activities observed per hour at night with 3.7 activities per hour recorded during the day and 9.9 activities per hour at night (Figure 5.3b). Peak activity rates formed a weaker bimodal pattern than that displayed in the observation enclosure. Peak activity rates were from 1700 hours to 0000 hours at night, while a much smaller period of activity was also observed at 0600 hours to 0700 hours in the morning (Figure 5.3b).

In the observation enclosure it was found that overall, the total number of activities observed during daylight hours over 72 hours for each behaviour were not significantly different from that observed at night (Table 5.3). However, the Templeton data showed that the main behaviours contributing to the increase in activity at night were *active*, *active and vocalising*, *moving*, *moving and vocalising*, and *drinking* (Table 5.3).

Proportionately, the observation enclosure data showed that the most frequent behaviours were *active* and *moving* and if combined, they accounted for 66% of all activity (Table 5.4). On average, most behaviours lasted less than 3 minutes at a time (Figure 5.4a) The mean time the ferret took to feed (*eating*) during the day was significantly longer than feeding at night ($F_{6,661} = 3.75$; $p = 0.001$). However, mean activity times between day and night for all other behaviours were not different ($F_{1,661} = 2.18$; $p = 0.14$: Figure 5.4a). Table 5.5 shows the maximum and minimum times recorded for the individual behaviours. The maximum time in any one behaviour was generally less than 15 minutes, although two behaviours, *active and calling* and *moving*, continued for more than 50 minutes.

As with the observation enclosure, the ferret spent most of its active time *active* and *moving*. These two behaviours accounted for 59% of all activity, even when an additional two behaviours (*female contact* and *male contact*) were added (Table 5.4). On average, most behaviours lasted less than 2 minutes at a time (Figure 5.4b). The mean time spent

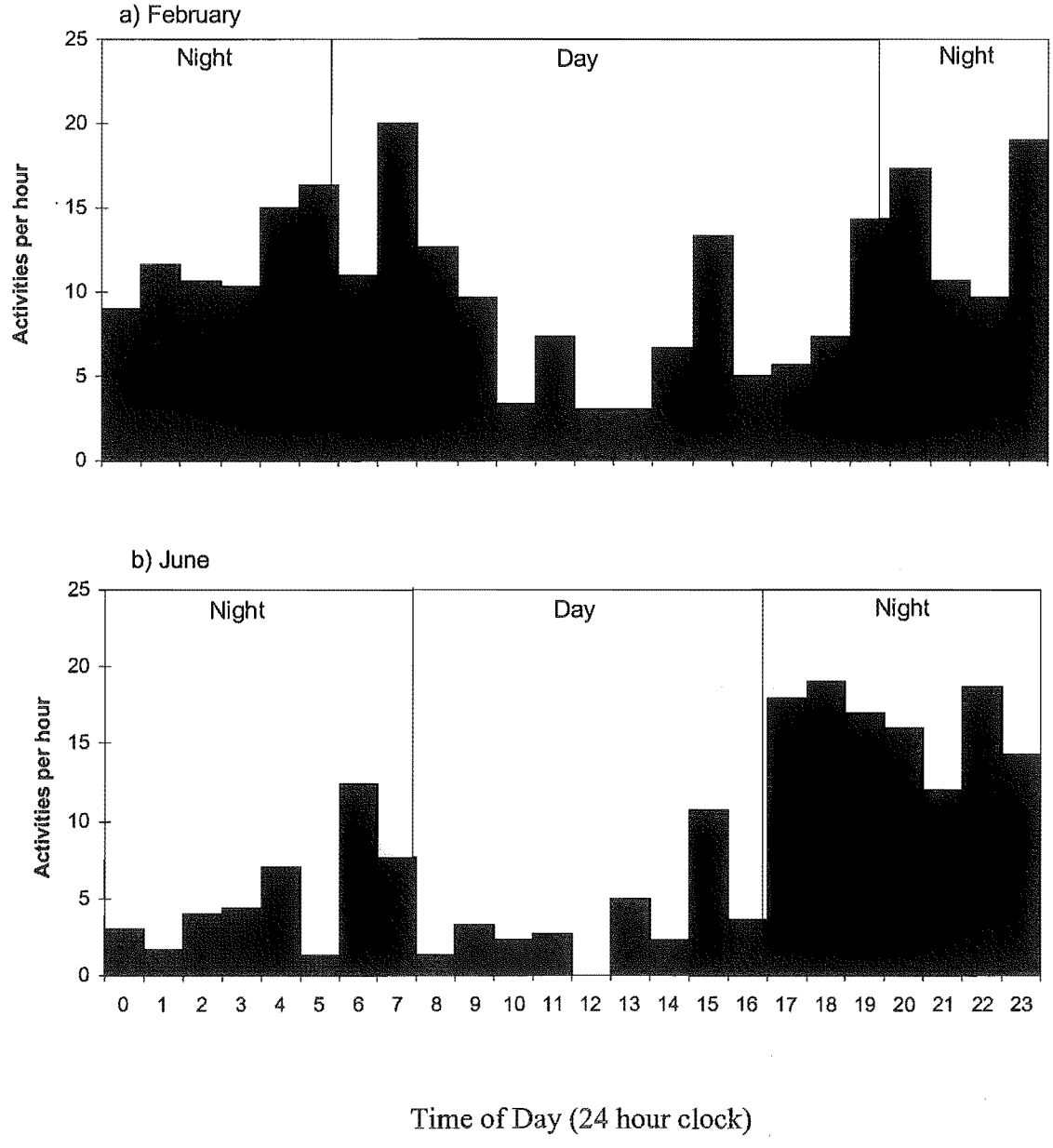


Figure 5.3. Frequency of behaviours (activity rate) of the ferret per hour in a) the observation enclosure and, b) at Templeton. (Data averaged from 72 hours of observations).

Table 5.3. Number of day and night activities of the ferret over 72 hours of observations for a) the observation enclosure and b) at Templeton. Contingency table data (G-tests) were used to test the null hypothesis that the number of activities during the day were the same as those at night.

Location	Behaviour	Number of Activities		G-Test
		Day	Night	
a) Observation Enclosure				
	Active	106	99	0.24
	Active and vocalising	25	16	1.99
	Defecating or urinating	20	24	0.36
	Drinking	47	64	2.61
	Eating	9	18	3.06
	Digging	11	21	3.18
	Moving	108	108	0
	Sleeping/inactive	41	39	0.05
b) Templeton				
	Active	42	126	43.95 ***
	Active and vocalising	15	42	13.32 ***
	Drinking	11	28	7.66 **
	Eating	9	18	3.06
	Female contact	5	10	1.7
	Digging	17	20	0.24
	Moving	55	120	24.73 ***
	Moving and vocalising	22	45	8.06 **
	Male contact	12	21	2.49
	Sleeping/inactive	13	27	5.01 *
	Transmission loss	1	20	21.07

(*p<0.05; **p<0.01; ***p<0.001)

Table 5.4. Number of activities per day and the proportion of activities observed for a) the observation enclosure and b) at Templeton.

Location	Behaviours	No. of activities per day	% activities per day
a) Observation Enclosure			
	Active	68	32
	Active and vocalising	14	6
	Defecating and urinating	14	7
	Drinking	24	11
	Eating	9	4
	Digging	11	5
	Moving	72	34
	Total No. of Activities	212	
b) Templeton			
	Active	56	29
	Active and vocalising	19	10
	Drinking	13	7
	Eating	9	5
	Female Contact	5	3
	Digging	12	6
	Moving	58	30
	Moving and vocalising	22	12
	Male contact	11	6
	Total Activities	205	

Table 5.5. Maximum and minimum activity times for each behaviour for a) the observation enclosure and b) at Templeton. Times represent hours: minutes: seconds.

Location	Behaviour	Minimum time per behaviour	Maximum time per behaviour	Total time per behaviour over 72 hours
a) Observation Enclosure				
	Active	00:00:05	00:09:58	04:50:21
	Active and calling	00:00:06	00:51:27	02:28:28
	Defecating & urinating	00:00:08	00:02:06	00:25:30
	Drinking	00:00:07	00:11:32	01:40:49
	Eating	00:00:10	00:11:41	01:23:43
	Digging	00:00:11	00:13:32	00:48:56
	Moving	00:00:04	01:01:22	05:16:20
b) Templeton				
	Active	00:00:05	00:18:09	04:26:09
	Active and calling	00:00:10	00:11:25	01:19:33
	Drinking	00:00:10	00:03:45	00:41:08
	Eating	00:00:16	00:06:29	00:49:25
	Female contact	00:00:15	00:07:43	00:30:19
	Digging	00:00:16	00:04:37	00:48:06
	Moving	00:00:08	00:09:25	03:50:11
	Moving and calling	00:00:09	00:09:12	01:52:39
	Male contact	00:00:16	01:03:03	02:11:25

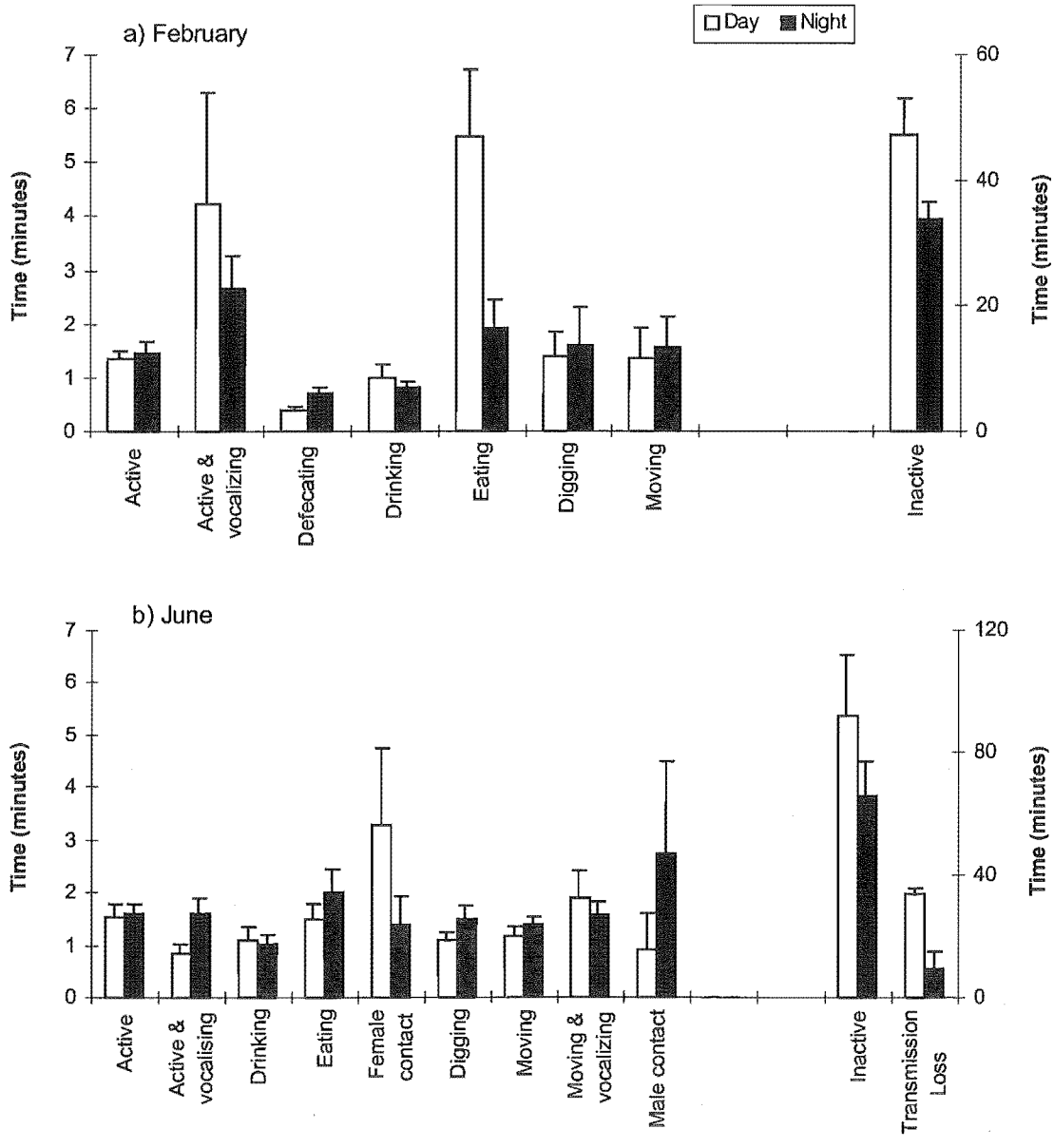


Figure 5.4. Mean activity times for each behaviour of the ferret during the day and at night for a) the observation enclosure and b) at Templeton. (NOTE: second axis for inactive/sleep. Error bars = ± 1 SE. Data averaged from 72 hours of observations).

between each behaviour did not differ significantly ($F_{8,600} = 1.00, p = 0.4328$). Again, similar to the observation enclosure, no significant differences in mean activity times for all behaviours were observed between day and night ($F_{1,600} = 0.49, p = 0.4819$: Figure 5.4b). Minimum and maximum times recorded for individual behaviours are shown in Table 5.5.

Intra-observer reliability comparing the sounds and behaviours of the ferret at Templeton from direct observations and the acoustic VCR recordings was $r_s = 0.966$ (n = 12, d.f. = 10).

5.4. Discussion

By using an all occurrence focal sampling technique on one ferret it was possible to produce an exact record of its behaviour. From this record, the time when a behaviour occurred, for how long a behaviour occurred, and the frequency of changing behaviours (activity rate) could be measured. It was also possible to accurately determine when the ferret was active or inactive. Moreover, by using an all occurrence sampling method in conjunction with ASTS technology, it was possible to gather information on rare and unusual behaviours that may have never been documented before or may not have been observable because the animal would move out of sight or underground.(Kenward 1987) Although several experimental design factors are compromised by only studying one subject, the decision to use only one ferret was a result of practical limitations and high development costs associated with this experimental technique. In addition, the logistics of trying to listen to more than one animal at a time in this experiment was impossible because of the large volume of sound data involved.

The total amount of time the ferret spent active in the observation enclosure was similar to that in the larger enclosure at Templeton. This suggests that wearing the ASTS collar and being held in captivity did not adversely affect the natural behaviour of the ferret. Activity budgets for other mustelid species also indicate similar activity patterns and periods of activity. For example, from variations in signal strength and pitch, Gerell (1969) found that mink (*Mustela vison*) in Sweden were active between 14-42% of the time and Zielinski *et al.*, (1983) found that pine martens (*Martes americana*) in the USA were active between 20-40% of the time. In an activity study in New Zealand, Medina-Vogel (1998)

found captive ferrets to be active 14% of the time during the non-mating season and between 16-19% of the time in the mating season.

Even though an animal may be out of sight to an observer (i.e., underground), the ASTS recordings show that the ferret was just as active during the day as at night. Therefore, just because an animal is underground does not mean it is inactive or resting. With the use of ASTS technology many activities normally performed underground could easily be heard (e.g., *moving, eating* and *female contact*). Medina-Vogel (1998) observed ferrets taking food into their dens but because they could not be viewed they were classified as resting. Thus, their feeding time would have been underestimated and resting time overestimated. Unfortunately, because ferrets are infrequently seen above ground during the day this has given rise to the hypothesis that they are nocturnal.

Generally, mean diel times for individual behaviours were not significantly different. That is, the time it took to perform a behaviour was the same regardless of whether it was during the day or at night. Although mean diel activity times were often similar, the actual number of behaviours performed during the day were sometimes different to those at night. For example, in June (winter), the activity rate of the ferret per hour was much less during the day than at night, yet the mean time it took to perform these behaviours was the same. Thus, in this example, the ferret was more active at night than during the day. However in February (summer), no difference was found between the number of activities performed during the day compared to the night.

Differences in monthly activity patterns are likely to result because of differences in the photoperiod length (Aschoff 1966; Woods and Kennedy 1997). The day-night cycle of illumination varies in Christchurch from 16 hours of daylight in the summer to 9 hours of daylight in the winter (Land Information, New Zealand 1998). To account for the varying photoperiod length, the number behaviours heard during the day should be divided by the number of hours of daylight, and vice versa for night activity. This conversion rate would then allow for the day and night activity of an animal to be compared between months.

The only behaviours that always had constant mean times were *inactive* and *defecating/urinating*. Among mammals, ferrets are moderately long sleepers and under laboratory conditions they were found to spend more than 60% of their time asleep (Marks and Shaffery 1996). Although the number of times the ferret slept did not differ in this study, the mean length of time spent sleeping at night was often shorter than during the

day, which could explain one reason why ferrets are considered nocturnal animals. As *defecation/urination* is a physiological response normally associated with an endogenous body rhythm and feeding behaviour (Hill and Wyse 1989), the lack of a difference between the number of times the ferret defecated or urinated is not surprising. The ferret(s) only defecated in a common latrine and sometimes after defecating they would be seen dragging their anal scent glands along the substrate or over a log. Ferrets use an anal drag behaviour as an olfactory means of scent marking their territory and for inter- and intrasexual communication (Clapperton 1989).

Ferrets are naturally inquisitive animals, and when active, are constantly on the move (Eibl-Eibesfeldt 1956). Consequently, many activity sequences were very short in duration. Thus, a major advantage of ASTS technology over conventional radio tracking is not so much knowing when the animal is moving but determining what it is doing when it is **not** mobile. For example, the ferret would wake up after a long period of inactivity, eat or drink for a minute or two and then resume resting. As eating and drinking are important measures in energy expenditure studies (Powell *et al.*, 1985), being able to ascertain the amount of time and when an animal spends performing these behaviours can assist in developing theories on energy expenditure and reproductive costs according to sex, age and season (Sandell 1989). Powell *et al.*, (1985), in their study on the energy expenditure of the black-footed ferret (*Mustela nigripes*), constructed a model which predicted that black-footed ferrets expend between 105-130 kcal day $^{-1}$ on average when temperatures were colder than 0° C. To construct this model they acquired much of their information from time budget observations. ASTS technology could further improve these models by providing more accurate time budget and behavioural information.

The main limitation of ASTS technology when studying small mammals, is the size of the battery and its life expectancy. The expected life of a ½ AA lithium battery, operating continuously, is only 10 days and for a ⅔ AA lithium battery, 13.5 days. Small batteries were required so the collar did not exceed the 5-6% of body weight as recommended by Tester (1971; cited in Kenward 1982). If larger animals were studied, larger batteries could be used thus extending the expected life of the ASTS. Similar problems were discussed in Greager *et al.*, (1979).

Using conventional radio tracking surveillance techniques to observe an animal in the wild can be incredibly difficult (Mech 1974), especially if the animal is likely to flee when it detects an observer (Kenward 1987). Although some animals may habituate to the

presence of an observer, even habituation may alter their natural behaviour (Martin and Bateson 1986). ASTS technology provides a powerful tool to remotely measure an animal's behaviour without necessarily being in visual contact at all times. Nevertheless, ASTS technology operates by line of sight, so a researcher needs to be in signal range (Greager *et al.,* 1979). In a field experiment to assess the performance of ASTS technology, I was able to receive, with excellent clarity, the sounds of blowflies (Family: Calliphoridae) ½ metre down a rabbit hole when standing on a small hill 1.5 km away. At 2 m above the ground, the height of someone holding a 3-element Yagi antenna at arms length, the signal could still be heard between 200-300 m away, while the signal increases dramatically when only 100 m away. If an animal is above ground, the signal can be heard from an even greater distance and, again, if the study subject is a large tree dwelling species then a researcher can easily listen to the animal without fear of disturbing it (M. Logan *pers. comm.*).

A second limitation associated with signal range and loss occurred when the ferret moved deep underground. Although some information was invariably lost, in many instances this loss was relatively short. Therefore, this information is still useful as it could be used to estimate what the animal was doing. For example, if the ferret was recorded as active before and after a short period of transmission loss, one could assume that the ferret was also active during this period. However, for reasons of accuracy, periods of transmission loss greater than 15 seconds should be recorded separately. This comes at a cost, as some underground activities, such as *female contact* and *eating*, may be under- or overestimated. If the audio signal was lost for a period greater than 20 minutes then it could be assumed that the ferret was *resting* or *inactive*. If a regular den is used, a microphone attached to wires could be installed inside the den to prevent this loss of audio signal. Intermittent periods of transmission loss also occurred when the ferret roamed near the wire fence. This was more a nuisance than a loss and would not normally occur in the field.

The cost of a conventional radio tracking transmitter is $312 (NZD) while the audio transmitter cost a further $172 (Sirtrack Ltd, Havelock North, New Zealand, 1999). Receivers and antennas are an additional cost. However, for the extra cost of using an audio transmitter, one buys many advantages over a conventional radio tracking system. These include information on specific behaviours (e.g., *feeding*), the length of time a behaviour occurs and the vocalisations of the study animal and conspecifics (Alkon and

Cohen 1986). In the past many researchers have had to rely on the integrity of the radio signal and pitch variations to estimate when an animal was active (see Sunquist and Montogomery 1973; Caley 1997), or what an animal may be doing (Mech 1983). ASTS technology surpasses this "educated-guess" technique and provides a robust method which reduces the uncertainty often associated with changes in signal character and strength.

The final limitation found with ASTS technology, was in interpreting and analysing the vast amount of data that can be obtained. Although the signal was digitised so it could be analysed by computer, the ferret's behaviours were best distinguished by ear and then recorded onto prepared check-sheets. ASTS technology is also best suited to animals that vocalise; however, it has been used to measure various sounds associated with certain behaviours, such as *eating*. Although elaborate sound recognition programmes exist, they may have great difficulty in analysing wildlife behaviour sounds that are not strictly vocalisations. Nevertheless, much of the data could be automated if certain sound parameters were identified and the problems associated with writing these complex algorithms conquered.

If an instantaneous sampling technique had been used in this study many behaviours that rarely occur may have been missed. Common to activity pattern studies, radio tagged animals are monitored for very short periods, at intervals of 20 minutes or more (see Thompson and Colgan 1994; White *et al.*, 1994). Although instantaneous focal sampling techniques have been identified as giving a good approximation to the proportion of time spent performing a behaviour (Tyler 1979), the length of the sampling interval should be as short as possible so as to not miss any rare and possibly quite important behaviours (Martin and Bateson 1986). However, the advantage of instantaneous time sampling is that it allows for more than one individual to be monitored at a time. Nevertheless, if the information gained from conventional radio tracking data is inaccurate because of a failure to detect bouts of activity, as found by Jacobsen and Wiggins (1982) in their study on white-tailed deer (*Odocoileus virginianus*), then continuous rather than instantaneous sampling should be used.

One major advantage with ASTS technology, not touched on in this chapter, is that many behaviours and vocalisations can be identified and analysed in bioacoustical programmes like CANARY® and Sound-Edit Pro®. Thus, functional aspects of an animal's vocalisations, such as encoding and decoding the meaning of a signal between sender and recipient, can be performed (Peters and Wozencraft 1989). Many unknown vocalisations

associated with infrequent behaviours such as mating, defensive and offensive calls could also be described. Furthermore, with bioacoustical programmes, it is also possible to measure the duration and frequencies of calls produced by an animal. Another advantage of ASTS technology is that sequences of common behaviours such as *drinking, moving, calling*, and even breathing (*snoring*) can be measured by a per unit time (i.e., as a rate of time).

While ASTS technology is not new, documenting the behaviour of an animal by listening to its vocalisations and activities is. It provides a new approach to unravelling many aspects of animal behaviour, especially on those that are considered elusive and nocturnal. It is not meant to, nor will it ever, replace direct observations and/or conventional radio tracking. Indeed, it is seen as a useful tool to be used in combination with conventional radio tracking systems. Additionally, ASTS technology is also not limited to observing only one animal, or to continuous sampling techniques. If sufficient resources are available, then many animals can be studied at the same time; however, measuring group interactions may still remain difficult. Finally, the full potential ASTS technology has yet to be explored and there are still plenty of hurdles to overcome, but with advances in technology, it is hoped that with this first step many research opportunities in behavioural ecology will unfold.

Chapter Six

Measuring the activity pattern and behaviour of a wild male ferret during the breeding season using an acoustically sensitive transmitter system.

6. Abstract

Understanding how ferrets (*Mustela furo*) behave under natural conditions, especially during the breeding season, may greatly improve trapping results. Several behavioural hypotheses have been proposed to explain why it is difficult to trap ferrets during the breeding months; however, documenting ferret behaviour has historically been restricted by technology. From June to December 1997, a focal sampling technique was used to investigate the behaviour and activity pattern of an adult wild male ferret using an acoustically sensitive transmitter system (ASTS). It was not only possible to determine when the ferret was active, but also what behaviour the ferret was performing, how long each behaviour occurred, and the sequence and frequency of behaviours. By using ASTS, crucial behaviours such as *eating, drinking, grooming, digging* and *female* or *male contact* could be easily identified. The two most variable behaviours recorded during the breeding season were *female contact* and *eating*, and could explain why ferrets are difficult to trap during the breeding season. It was found that the ferret *ate* less often and spent more time in *female contact* during September and October than in any of the other months recorded; resulting in the ferret possibly ignoring baited traps because of a preoccupation with breeding. In addition, the ferret was often active during the day and displayed an ultradian activity pattern; however, most activity during the day occurred when the ferret was underground, perhaps explaining why ferrets have previously been thought to be nocturnal. Nevertheless, because only one ferret was documented, results from this study are only suggestive of what feral ferrets may do in the wild.

6.1 Introduction

Ferrets (*Mustela furo*) were introduced into New Zealand last century as a biocontrol agent for rabbits (*Oryctolagus cuniculus*; (Thomson 1922; Wodzicki 1950). Unfortunately the experiment failed and New Zealand's ferret population has now grown to be the largest feral population in the world (Nowak and Paradiso 1983). Although widely regarded as a pest in conservation circles (Murphy 1996; Alterio and Moller 1997b), ferrets went unnoticed by most farmers until only recently. However, feral ferrets are an alternative host of bovine tuberculosis (*Mycobacterium bovis*: Tb) in New Zealand (Lugton *et al.*, 1997; Caley 1998), and because they help spread Tb and threaten meat exports, their presence is no longer tolerated by the farming community.

Several organisations, such as the Animal Health Board and the Ministry of Agriculture and Forestry, have in recent times assisted farmers in trapping ferrets to control their numbers (Oliver 1996). However, trapping has resulted in mixed success. Ferrets are generally easy to trap during summer and autumn, but can be extremely difficult to trap during their breeding season between September and December. Several hypotheses have been proposed to explain this seasonal variation (see Chapters 2 & 3), but to date, nobody has studied the behaviour of wild ferrets under natural conditions over the breeding period.

In addition to seasonal variation in activity, this study was also interested in the frequency and time a ferret spent performing certain behaviours each day. Ferrets, and their ancestral relatives polecats (*Mustela putorius*), are generally described as nocturnal. This hypothesis is debatable, with some authors arguing that ferrets are diurnal as well as nocturnal (Stockman *et al.*, 1985; Weber 1989a), while others state that ferrets are strictly nocturnal (Herrenschmidt 1982; Lodé 1995; Alterio and Moller 1997a).

However, before an activity pattern can be defined correctly, definitions for the terms nocturnal, diurnal, crepuscular and ultradian are needed. An animal is considered **nocturnal** if it is active between sunset and sunrise, and is considered **diurnal** if active from sunrise to sunset (Brady 1982). Conversely, if an animal is active mainly at dusk and dawn, then it is **crepuscular** (Brady 1982). **Ultradian** behaviour is defined as several short-term activity cycles occurring within a 24 hour period (Halle and Stenseth 1994). Ultradian patterns can vary from several minutes to several hours and their duration is independent of circadian cycles (Gerkema and Daan 1985). Ultradian activity rhythms have been known in animals for many years and most are related to physiological

processes; as a result, many researchers have found it easier to study circadian rhythms (Kleitman 1985).

Conventional wildlife radio tracking involves capturing an animal, fitting it with a radio collar, then releasing it back into the wild so that it can be remotely monitored (Mech 1983). The objective is to then systematically collect data on the movements, including home range and territory, and behaviour of the animal (Sargeant 1980). Radio telemetry, although excellent for locating animals, makes gathering behavioural information difficult. With radio telemetry, a researcher must get close enough to observe the animal without disturbing it (Kenward 1987); however, even if one can observe an animal without unduly affecting its behaviour, the animal may often move in and out of sight or underground, making records incomplete (Mech 1974). Additionally, behavioural studies using radio telemetry have been made even more difficult if the animal is considered nocturnal (Alkon and Saltz 1988).

Although radio telemetry has also been used by Mech (1974), Niemimma (1995), and Alterio and Moller (1997a) to describe animal activity patterns, only variations in signal strength, pitch or pulse rate are collected (Kenward 1987). As a result of direct observation not always being possible, radio telemetry cannot verify what an animal is actually doing (see Sunquist and Montogomery 1973; Caley 1997). Therefore, caution must be taken in interpreting radio telemetry data that is limited to whether the animal is simply active or inactive. Not only does amplitude vary, as a result of changes in the orientation of the antenna (Kenward 1987), activities such as *eating* may produce an identical signal to *moving* (Greager *et al.,* 1979).

One method of reducing the above problem is to use an acoustically sensitive transmitter system (ASTS: (Greager *et al.,* 1979). ASTS technology remotely records the sounds and vocalisations made by an animal, and these sounds can then be associated with certain behaviours (see Chapter 5). Many sounds and their associated behaviour(s) are easily recognisable; nevertheless, some sounds require further identification. To do this, sounds of wild animals held in captivity can be simultaneously recorded with video images, and then calibrated with the associated behaviours of the animal in the wild (see Chapter 5 for a review).

One major advantage of ASTS technology is that it can be used to build a complete and faithful record of the time an animal spends involved in each activity (see Chapter 5). This type of information could be useful in developing models in relation to a predator's

food habits (e.g., their time spent acquiring food), whether seasonal changes affect activity (e.g., winter versus summer), movement (e.g., the time spent moving per hour, over 24 hours), time-energy budgets and energy expenditure (e.g., the time and energy spent in reproduction), and trapping success (e.g., when are predators active and likely to be caught).

Acoustic biotelemetry, although used by Owren *et al.*, (1997) on primates, Ford (1989) on cetaceans, and Nelson and Croner (1991) on bird vocalisations, has not as yet evolved to the stage where study animals can wear the audio transmitters (Alkon and Cohen 1986). Most acoustical studies have concentrated on vocalisation or responses to play-back experiments (Hopp *et al.*, 1998). To date, no study has attempted to measure an animal's activity pattern using remotely monitored audio equipment. This study investigates the behaviour and activity patterns of an adult male ferret fitted with an ASTS collar. The objective was to examine behavioural sounds and noises created by the ferret to determine: a) when it was active, b) what it did over a 24 hour period, and c) if the ferret's behaviour changed during the breeding season.

6.2. Methods

6.2.1. Study site and enclosure

The study ran from June to December 1997; however, data from July was omitted because of a technical failure. A 100 m x 75 m predator-proof enclosure, situated at Templeton near Christchurch, New Zealand, was used for the ASTS study. A full description of the enclosure is provided in Chapter 5.

6.2.2. Recording Protocol

Ideally, a replicated study would have been desirable, but several factors necessitated the need for studying only one animal. These were: a) availability of only one large predator-proof enclosure, b) limited budget available for audio transmitters, receivers and recording equipment, c) only one ferret could be tracked at a time with the equipment available, and d) limited time available for recording each session and analysing the data.

Before each recording session the ferret was given four days to acclimatise in the enclosure. The day before a recording session, the ferret was trapped and an ASTS collar was fitted so the equipment could be tested. The collar used in the recording sessions not

only had an acoustic transmitter, it also had a locator beacon so that the ferret could be tracked to a den. The life expectancy of the battery was ten days; however, with a locator beacon this was shortened to nine days. All recording sessions started at 10.00 am following the day of fitting.

A focal sampling technique was used to follow one adult male ferret continuously for a period of 96 hours each month. Although 96 hours of data were recorded only a period of 72 continuous hours (three full days) were analysed. The extra 24 hours per month was a security in case of a recording failure.

A full description of the recording equipment and protocol is given in Chapter 5. However, instead of two female ferrets inside the enclosure, five females with locator collars were released. A second male inside a small cage was also present. During the recording sessions, food was provided at random times and in different locations, either during the day or night.

a) ***Assumptions and definitions***

1. Aside from the behavioural categories defined in Chapter 5 (Table 5.2), no other behavioural categories were observed. Thus, the sounds and vocalisations identified in Chapter 5 are assumed to be the sum total of ferret activities and behaviours.
2. Each behavioural unit was regarded as mutually exclusive.
3. All active behaviours were divided into those that occurred during the day (diurnal behaviour) and those that occurred during the night (nocturnal behaviour). The times of sunrise and sunset delimited the diurnal phase; the twilight of dusk and dawn was included in the nocturnal phase from sunset to sunrise (New Zealand Standard Time).
4. *Transmission loss*, including when the ferret was underground or near the fence, was only recorded if there was a total loss of sound longer than 15 seconds in duration. If a behaviour, for example *active*, could be heard between intermittent bursts of signal loss, it was recorded as *active with intermittent periods of transmission loss* (see Table 5.2).

b) ***Data Management and Analysis***

As there was large variation in activity times, $\log_{10}$ transformations were used to normalise the data. Although some heteroscedasticity of variance did exist, the effect of moderate heterogeneity of variances are not too serious for the overall test significance (Sokal and Rohlf 1981). Nevertheless, as these results apply to only one animal, care has to be taken in interpreting these findings.

All time budgets and activity rate graphs were prepared from the 72 hours of observation data for each month. From this monthly data, comparisons were made between the breeding season, from September through to December, and the non-breeding season, from June until August, to determine if the time budgets and activity rate of the ferret altered between seasons.

Analysis of variance was used to test the null hypotheses: a) that mean activity times between diurnal and nocturnal behaviours would remain the same for each month, b) that the mean duration of each behaviour for individual months was the same and, c) that the ferret's behaviour would remain same between breeding and non-breeding seasons. Tukey HSD post hoc tests, with unequal sample sizes, were used to identify *a posteriori* multiple comparisons between all possible pairs of means.

To determine if more activities were performed by the ferret during daylight hours than at night, G-Tests for contingency table data (log likelihood ratio tests) were used for each month (Zar 1999). However, in comparing months, the number of activities heard were converted into rates to take into account the varying number of day and night hours. For example, the day activity rate was calculated as:

$$\text{Daily activity rate} = \frac{\text{the number of behaviours during daylight hours}}{\text{number of daylight hours}}$$

and vice versa for the night-time activities. For all other analyses, the actual activity rate of the ferret equalled the number of times the ferret changed from one activity (behaviour) to another activity (behaviour) per hour.

6.3. Results

Three examples of the ferret's activity pattern over 72 hours are shown in Figure 6.1. In June, most activity occurred at night, but by November the ferret's activity cycled every 2-4 hours. These graphs show no common activity pattern and activity changes with season. Thus, ferret activity was neither nocturnal, diurnal nor crepuscular.

Although no common activity pattern was detected from the 72 hour time budgets, the mean daily time budgets for each month suggest that the ferret generally had two main periods of activity: one in the early morning and another in the early evening (Figure 6.2). However, the ferret could be very active outside of these two main periods of activity. For example, in September and October, most ferret activity occurred in the early evening and

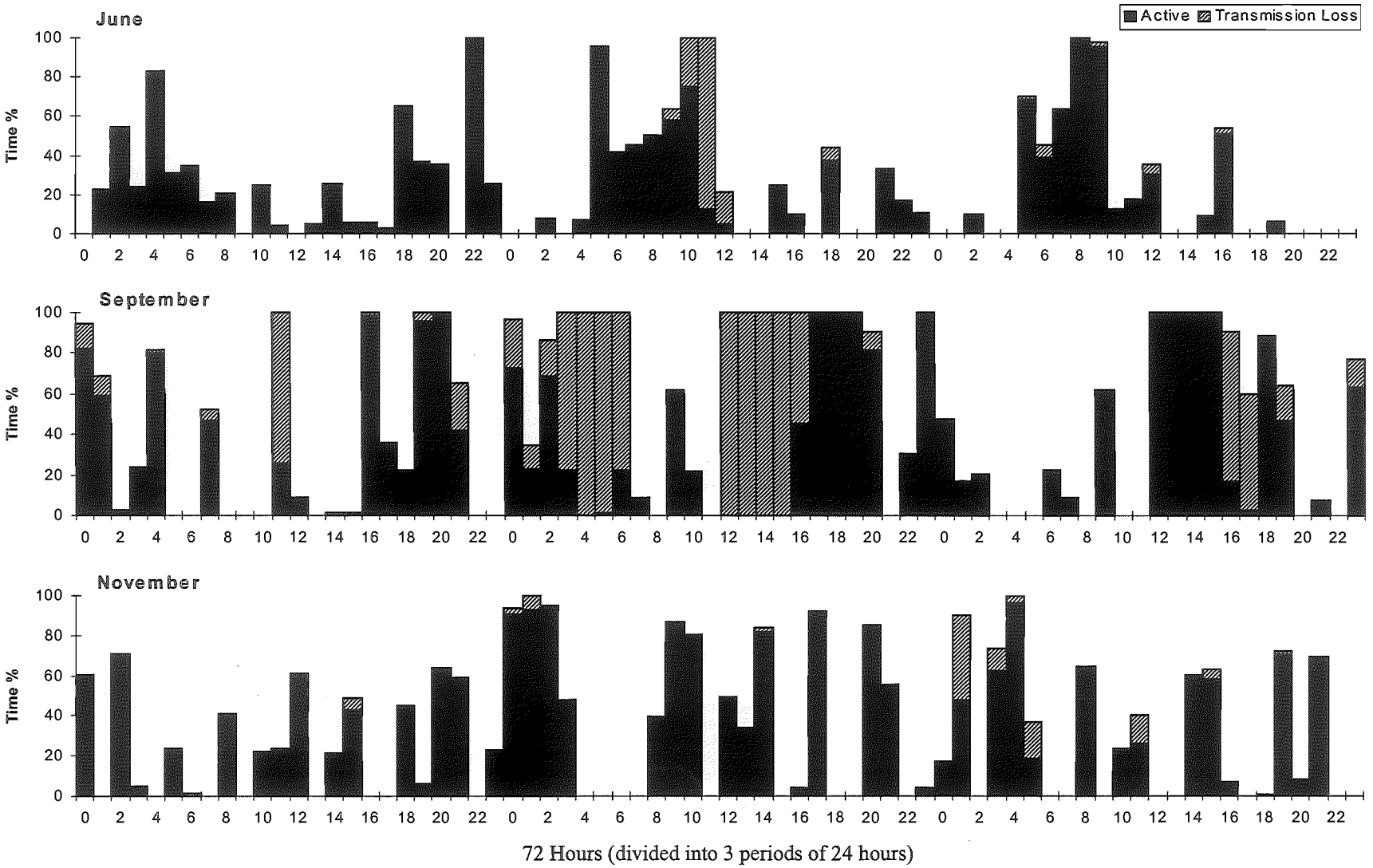


Figure 6.1. Percent of time spent active (activity budget) over a 72 hour period for June, September, and November (0 = Midnight; 12 = Midday)

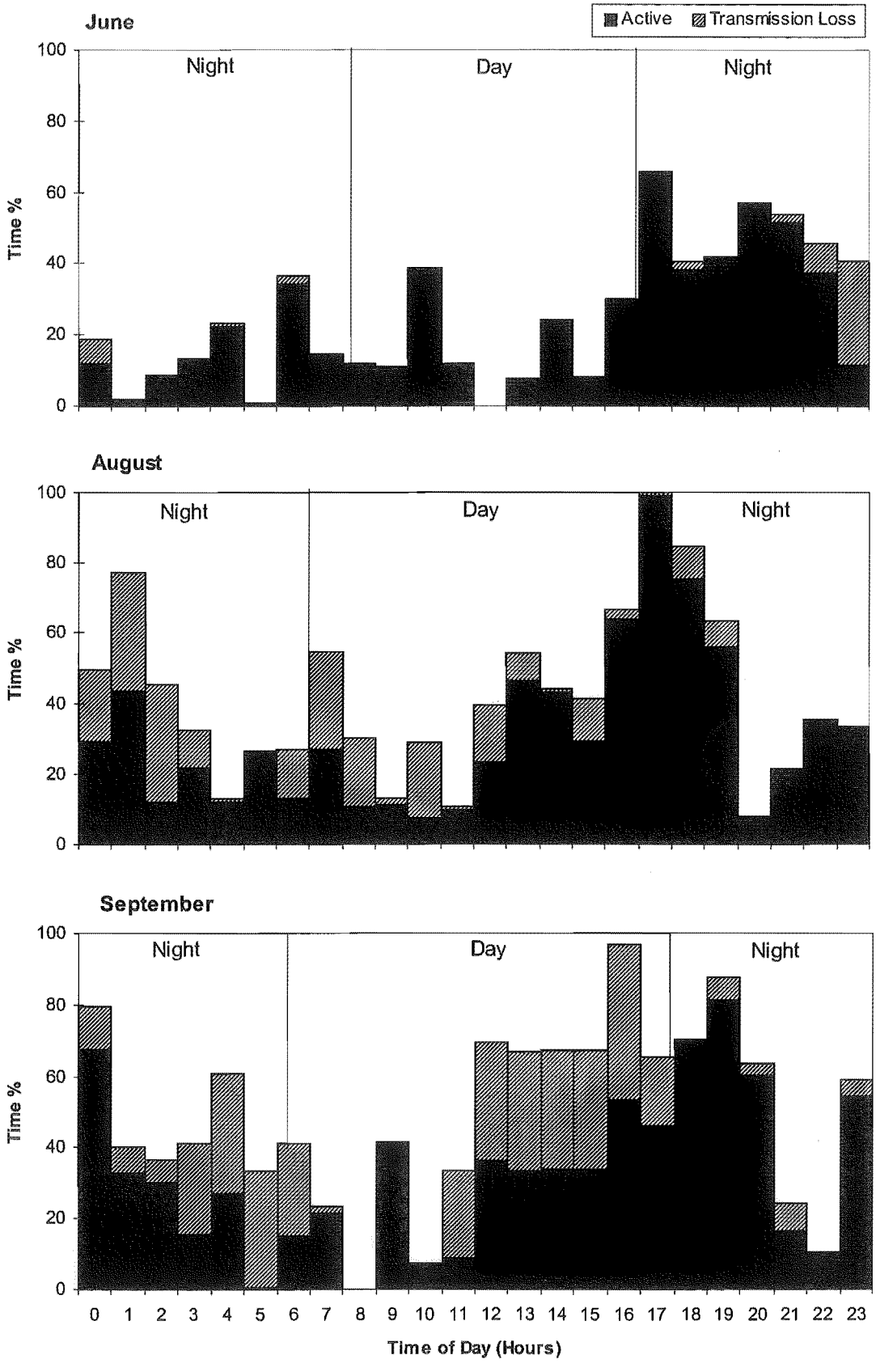


Figure 6.2. Daily time budgets of the ferret depicting seasonal changes in activity. (Data averaged from 72 hours of observations per month; 0 = Midnight; 12 = Midday).

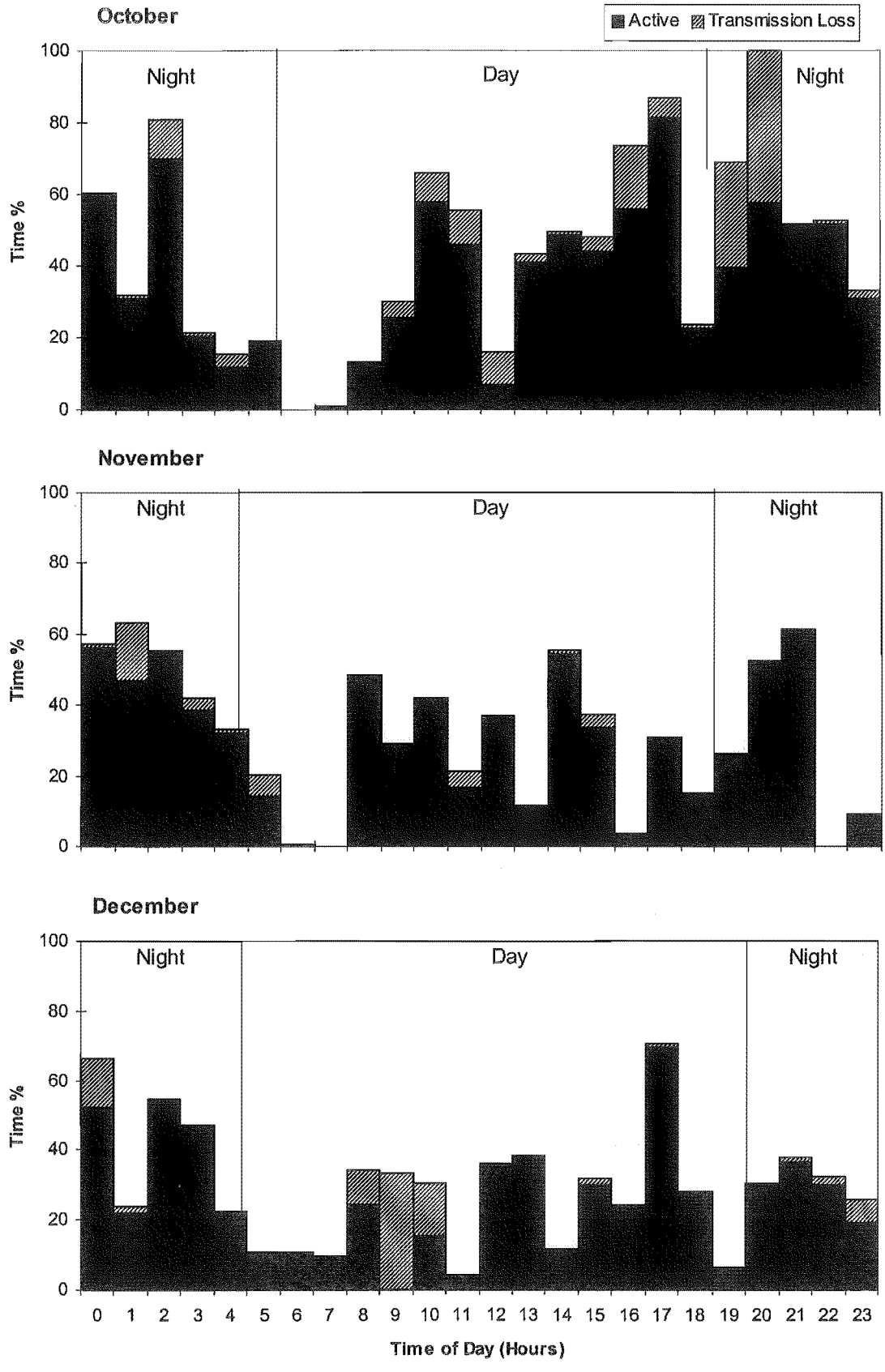


Figure 6.2 (cont.). Daily time budgets of the ferret depicting seasonal changes in activity. (Data averaged from 72 hours of observations per month; 0 = Midnight; 12 = Midday).

early morning, but he also had substantial periods of activity at other times during the night and day. Additionally, in November and December, the two peak periods of activity seen in previous months are not as visible.

Ferret activity from August to October mainly occurred between 1200-2000 hours, with a peak of activity near dusk (between 1700-1900 hours). Much of this activity was associated with the ferret *moving* or during *female contact*. During November and December when the nights were shorter, there was no early evening peak as found in June, when the nights were longer (Figure 6.2). In total, the ferret was active for 22% of its time in June (e.g., 16 hours, 8 minutes/72 hours) and in August 26% of its time. However, it was most active in September (34%) and October (38%). Activity started to decline again in November (31%) and December (29%). Interestingly, the overall proportion of time spent active during the day, for all six months, was only slightly less than at night (Figure 6.3).

Daily time budget graphs indicate that the ferret was more active during the day in the breeding season than in the non-breeding season (Figure 6.4). Mean daylight activity from 0800 to 1600 hours during the breeding season was 34% (SE = 3.13%), whereas it was only 18% (SE = 1.7%) during the non-breeding season. The lowest period of activity during the breeding season occurred between 0300 and 0800 hours and no prominent peak period of activity was apparent. However, during the non-breeding season, most activity occurred in the 8 hours after dark (between 1600 to 2300 hours), with a peak at 1700 hours. Only low levels of activity occurred in the other 16 hours during the non-breeding season. However, it should be pointed out that the non-breeding season is only represented by two months of data, both of which are winter months.

The activity rate, or the number of activities per hour, generally follows the same patterns observed in the time budget graphs (Figure 6.5). Mean activity rate per hour for the six months was 8.12 (SE = 0.74); however, this rate varied depending on whether it was day or night. When comparing the activity rate of daylight hours to those heard at night, a number of differences were observed (Table 6.1). Little difference was found between the activity rates of day and night observed in August and October; however, during June and September, the ferret was more active at night than during the day. Conversely, in November and December the number of activities during daylight hours were greater than at night. The three most distinct behaviours where diurnal activity differed from nocturnal activity were *active, moving, and moving and calling* (Table 6.1).

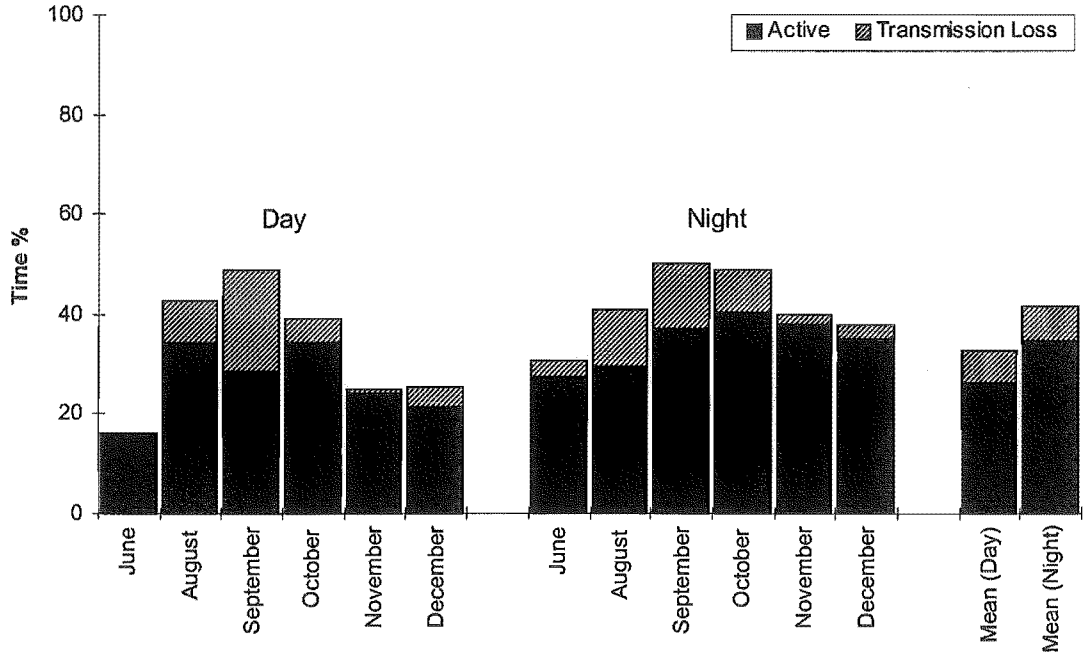


Figure 6.3. Proportion of time active during the day and night (Data averaged from 72 hours of observations).

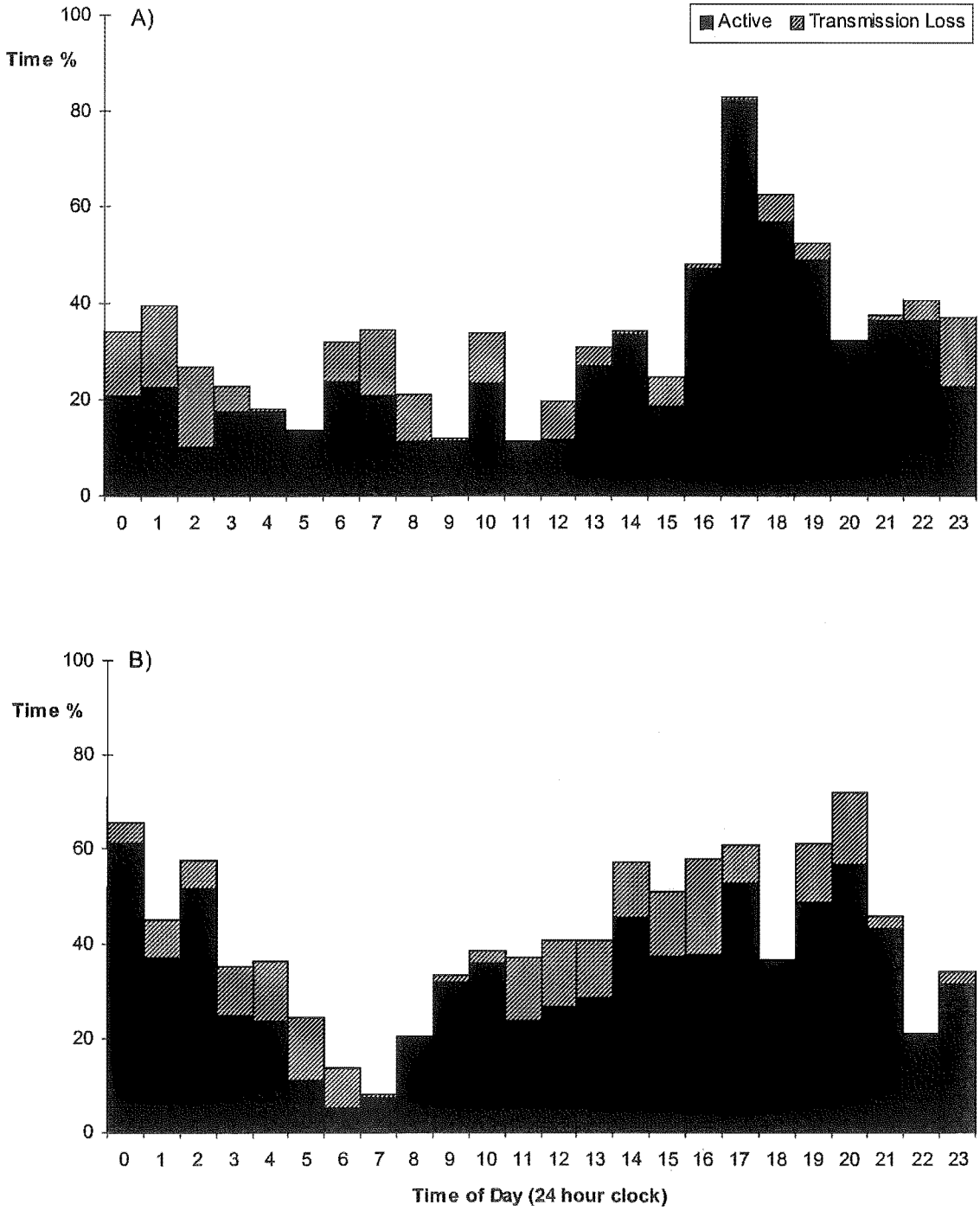


Figure 6.4. Activity budget of the ferret during: A) the non-breeding season and B) the breeding season.

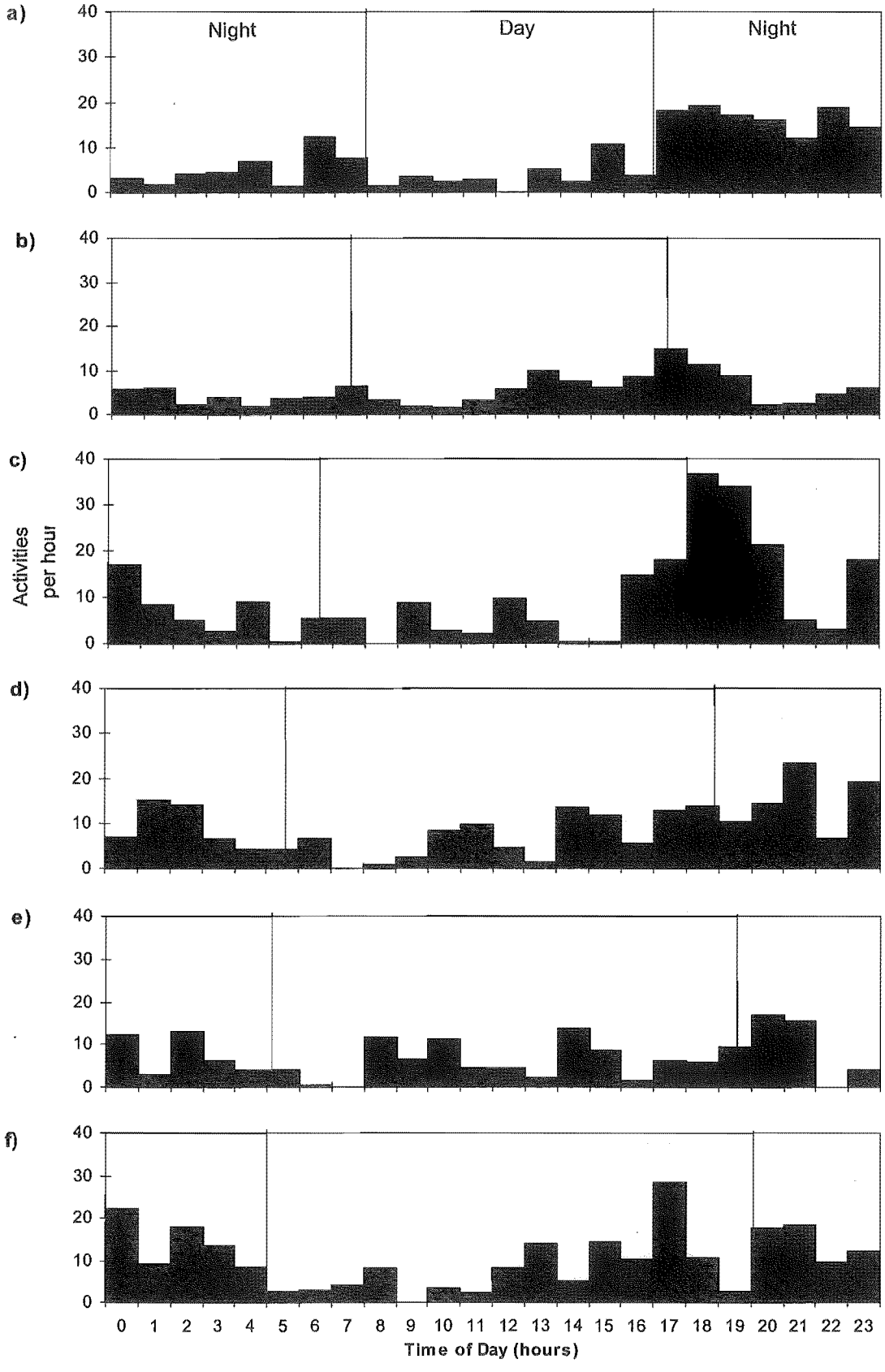


Figure 6.5. Seasonal change in activity rate per hour for the ferret.
(Data averaged from 72 hours of observations.
A = June, b = August, c = September, d = October, e = November, f = December).

Table 6.1. Day and night activities of the ferret. G-Test[1] = day vs night activities for each behaviour per month. G-Test[2] = comparative activity rates taking into account the number of daylight and night-time hours for each behaviour (from 72 hours of observations).

Behaviour	Month	Activities		G-Test[1]		G-Test[2]	Month	Activities		G-Test[1]		G-Test[2]
		Day	Night					Day	Night			
	June						October					
Active		42	126	43.95	***	1.08		63	77	1.4		0.39
Active/vocalising		15	42	13.32	***	0.29		33	41	0.87		0.23
Drinking		11	28	7.66	**	0.14		10	12	0.18		0.06
Eating		9	18	3.06		0.02		6	15	3.98	*	0.47
Female contact		5	10	1.7		0.01		30	18	3.03		0.11
Digging		17	20	0.24		0.1		46	30	3.39		0.11
Moving		55	120	24.73	***	0.25		91	106	1.14		0.42
Moving/vocalising		22	45	8.06	**	0.06		34	54	4.59	*	0.71
Male contact		12	21	2.49		0		12	17	0.87		0.16
Sleeping/inactive		13	27	5.01	*	0.04		10	12	0.18		0.06
Transmission loss		1	20	21.07	***	1.22		35	24	2.06		0.05
	August						November					
Active		97	96	0.01		0.13		66	35	9.67	**	0.18
Active/vocalising		15	16	0.03		0.01		12	7	1.33		0.02
Drinking		15	9	1.52		0.22		23	11	4.33	*	0.11
Eating		19	25	0.82		0.01		35	17	6.36	*	0.15
Female contact		14	15	0.03		0.01		30	20	2.01		0
Digging		9	8	0.06		0.03		19	10	2.84		0.05
Moving		118	100	1.49		0.5		51	23	10.86	** *	0.31
Moving/vocalising		48	38	1.17		0.29		98	48	17.47	** *	0.41
Male contact		1	2	0.34		0.02		4	2	0.68		0.02
Sleeping/inactive		19	25	0.82		0.01		26	11	6.26	*	0.2
Transmission loss		36	20	4.64	*	0.64		9	12	0.43		0.17
	September						December					
Active		55	129	30.62	***	2.55		105	52	18.25	** *	0.12
Active/vocalising		26	56	11.23	***	0.94		33	30	0.14		0.23
Drinking		5	14	4.44	*	0.37		29	21	1.29		0.04
Eating		16	18	0.12		0.01		46	22	8.66	**	0.07
Female contact		14	42	14.65	***	1.22		18	7	5.01	*	0.09
Digging		10	56	35.35	***	2.95		31	20	2.39		0.01
Moving		46	103	22.37	***	1.86		58	15	27.05	** *	0.9
Moving/vocalising		34	70	12.72	***	1.06		101	70	5.65	*	0.08
Male contact		2	0	N/A		N/A		35	40	0.33		0.67
Sleeping/inactive		13	25	3.86	*	0.32		26	13	4.42	*	0.03
Transmission loss		11	23	4.33	*	0.36		14	9	1.1		0

(*p<0.05; **p<0.01; ***p<0.001)

The mean number of diurnal activities observed over a 24 hour period in June was 62, whereas, in December it was 152 activities. Conversely, the mean number of nocturnal activities in June was 144, whereas, in December it was 92 activities (Figure 6.6). However, when the seasonal day/night cycle of illumination was taken into account between months, no difference was found between the number of activities for each behaviour during the day or night (Table 6.1).

The mean activity rate during the day, in the non-breeding season, was 5.5 activities per hour (SE = 1.40) and at night was 7.4 activities per hour (SE = 1.06), while in the breeding season, the mean activity rate during the day was 7.4 activities per hour (SE = 1.22) and at night was 10.7 activities per hour (SE = 1.47). The activity rate of the ferret during the day was significantly less than at night during the non-breeding season (G = 7.4, d.f. = 1, $p = 0.01$). During the breeding season, no difference was found between the number of activities observed during the day compared to the night (G = 1.04, d.f. = 1, $p = 0.05$: Figure 6.7).

From June to December, no overall difference was found between diurnal activity time and nocturnal activity time ($F_{1,3655} = 0.79$, $p = 0.37$). However, the mean time the ferret spent performing some behaviours did vary between day and night (Figure 6.8). Significant differences were found between *active and calling, digging, male contact* and *female contact* (Table 6.2). For example, the ferret spent more time *active and calling* at night in June and November and *digging* longer at night in August and September. Conversely, the ferret spent more time in contact with the other ferrets in the enclosure during the daytime. Most *female contact* was heard during the day when the ferrets were underground. The longest period of *female contact* was heard in September during the day when the male was with a female for a period of 2 hours 46 minutes. During this time, the male was heard to mate with the female. In October, the ferret mated successfully on two other occasions. Coitus in both instances lasted for more than an hour. *Male contact*, on the other hand, occurred above ground as the second male was kept caged.

Seasonally, the ferret devoted more time to some activities than others ($F_{7,3655} = 19.97$, $p = 0.0001$). This was particularly evident during the breeding season, especially in October when he spent a considerable amount of time in contact with the female ferrets (Figure 6.8). October was also different for several other behaviours. The ferret spent, on average, less time *eating*, more time *sleeping*, and was generally less *active* than for most other months (Table 6.2).

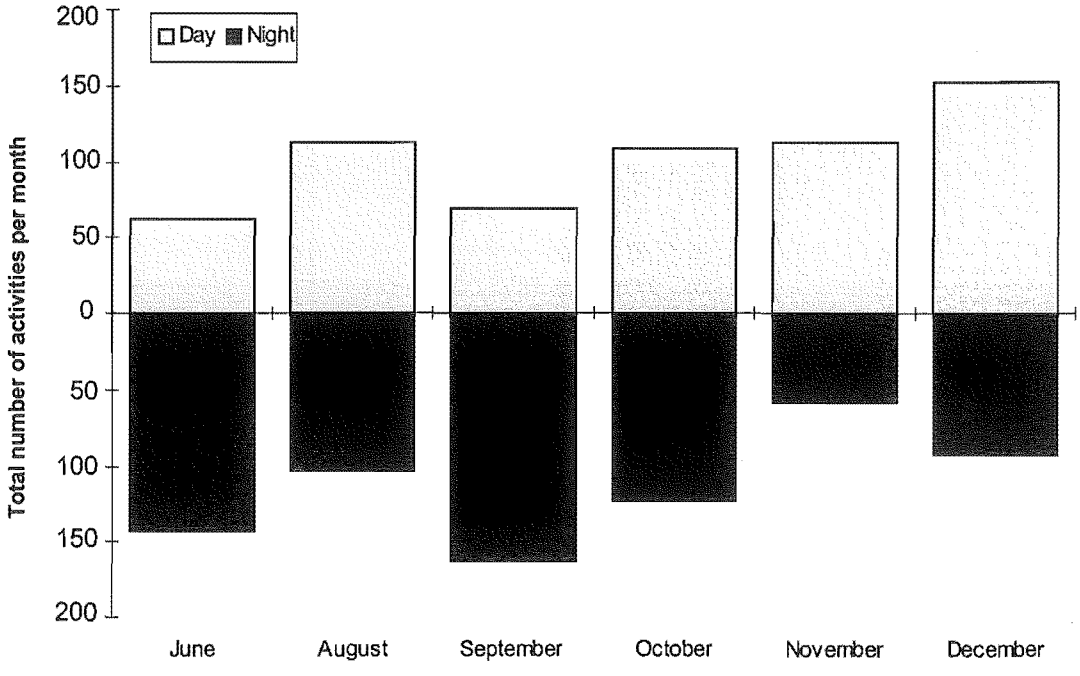


Figure 6.6. Total number of diurnal and nocturnal activities for each month (over a 72 hour period).

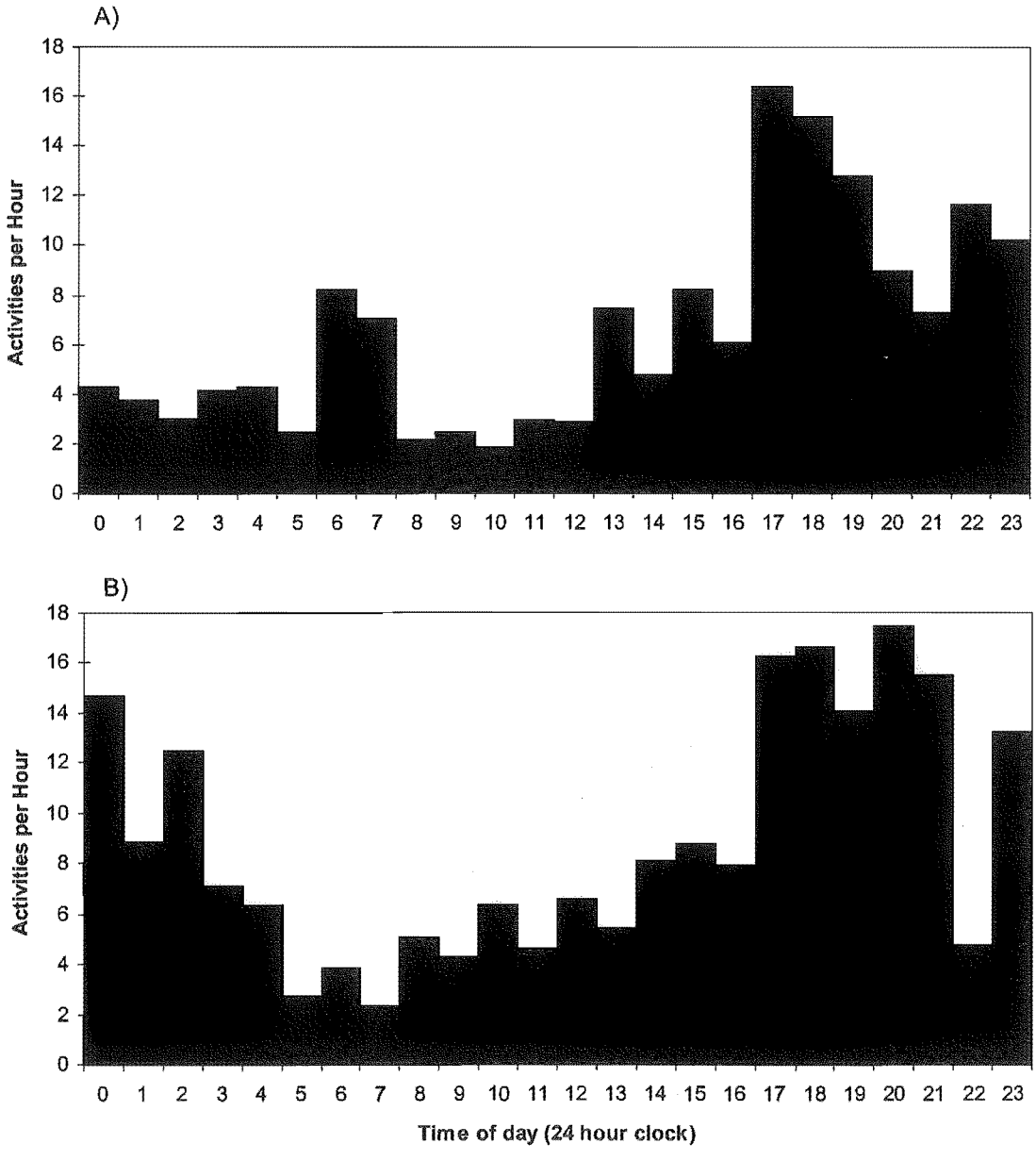


Figure 6.7. Activity rate of the ferret during: A) the non-breeding season and B) the breeding season.

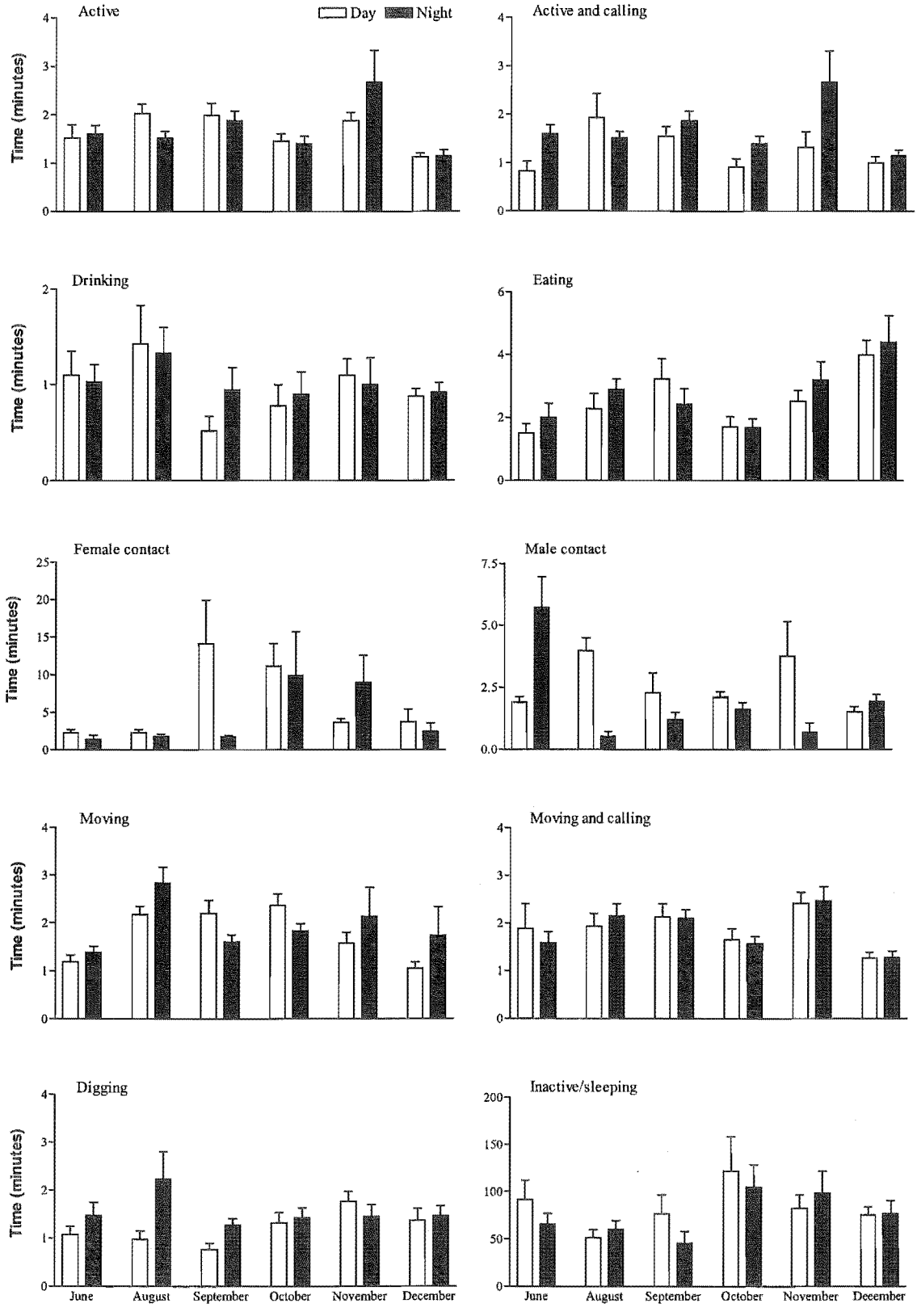


Figure 6.8. Mean time and standard error for diurnal and nocturnal activity for each behaviour. (Data averaged from 72 hours of observation).

Table 6.2. ANOVA results of the mean duration between day and night and season for each behaviour (Note: because only one ferret was used caution is required with these results).

	Day vs Night				Month			
	df Effect	df Error	*F*-value	*p*-level	df Effect	df Error	*F*-value	*p*-level
Active	1	931	0.09	0.764	5	931	5.90	0.000
Active and calling	1	315	4.40	0.037	5	315	3.36	0.006
Drinking	1	176	0.41	0.524	5	176	2.03	0.077
Eating	1	234	0.03	0.856	5	234	3.66	0.003
Female contact	1	211	4.85	0.029	5	211	2.82	0.017
Digging	1	264	4.94	0.027	5	264	1.88	0.099
Moving	1	874	0.17	0.677	5	874	15.62	0.000
Moving and calling	1	650	1.03	0.310	5	650	9.48	0.000
Male contact	1	131	4.79	0.030	2	131	0.91	0.405
Inactive/sleeping	1	208	0.61	0.434	5	208	3.74	0.003

Proportionately, the most common behaviours during a 24 hr period were those associated with the two behaviours *moving* and *active* (Figure 6.9). Together they accounted for 65% of the time the ferret was active. There were several other instances when the mean duration of behaviours changed with season (Figure 6.8). In June, the ferret spent less time *moving* around the enclosure than in August, and in December the ferret spent less time *moving and calling* than in November. The ferret also spent shorter periods *eating* in October, but longer periods in November and December.

Over a 24 hour period the ferret would, on average, spend 10 times *drinking* and 14 occasions *eating*. However, this varied according to month (*drinking* max: 17 times per day in December, min: 6 times per day in September; *eating* max: 23 times per day in December, min: 7 times per day in October). Contact with other ferrets showed the greatest variation for the proportion of time of any behaviour (range; 3.0% in June and 33% in October, $\bar{x} = 15\%$, SE = 4.91%).

Although the ferret was *inactive* for approximately 15 hours per day, the ferret did not sleep for one long continuous period. Instead, the ferret had between 7 to 15 sleeping episodes (*inactivity*) over a 24 hour period, ranging from 2 minutes to almost 7 hours (Figure 6.10), while the average *inactivity* period was one hour and 17 minutes (Figure 6.8). Although no difference was found between the amount of time spent *inactive* during the day compared to night ($F_{1,208} = 0.61, p = 0.43$), seasonal differences in the ferret's *inactivity* (sleep) patterns were observed. In August, the time *inactive* was significantly shorter than in October, because the ferret would spend considerably more time *moving* around the enclosure and in *male contact*. Additionally, during August, much of the time the ferret spent *digging* was when he was near the second male, suggesting that *digging* is possibly a form of territorial behaviour. As a consequence, the time spent *digging* and in *male contact* also contributed to less *inactivity* (sleeping) time.

Most periods of *transmission loss*, mainly associated with the ferret moving deep underground, were short in duration (< 15 seconds). However, of the times when *transmission loss* was greater than 15 seconds, the mean period of *transmission loss* was 8 minutes. In several instances during the *transmission loss* periods, the ferret could be heard. However, as the sound quality was so poor, a definite behaviour could not be attributed to the sound(s). This was particularly apparent during two long periods of *transmission loss* in August and September, when the occasional sound could be heard but not identified.

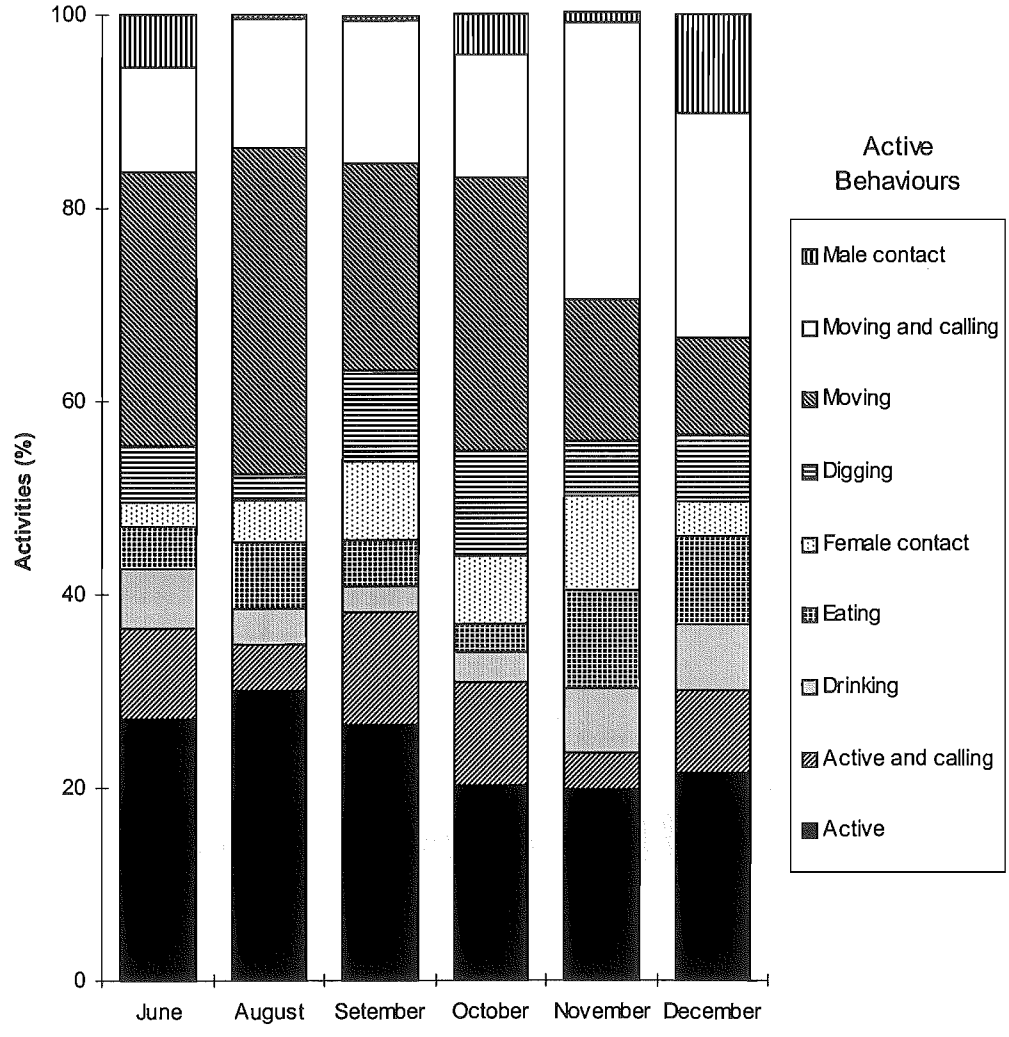


Figure 6.9. Proportion of active behaviours performed by the ferret over a 24 hour period. (Data averaged from 72 hours of observations for each month).

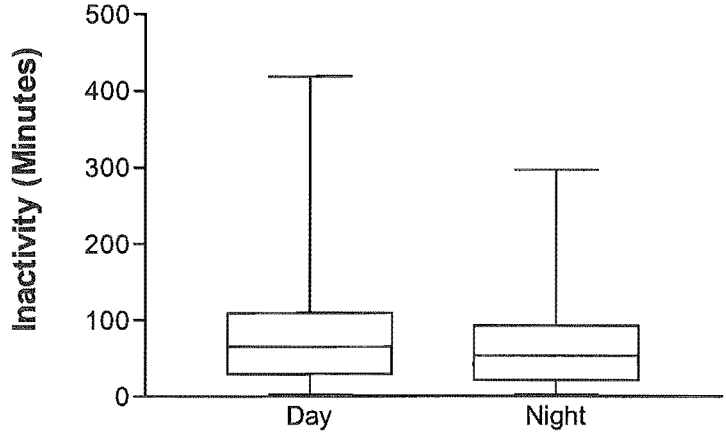


Figure 6.10. Duration of ferret inactivity. Data from 72 hours of observations per month and then averaged for the six months. The box extends from the 25th percentile to the 75th, with a horizontal line at the median (50th percentile). Whiskers extend down to the smallest value and up to the largest.
Day versus night = not significant: $F_{1,208} = 0.61$, $p = 0.43$.

6.4. Discussion

Although generalisations about the behaviour of one animal can be misleading because of the diversity and variability normally found in nature (Martin and Bateson 1986), care has been taken not to extrapolate my results to all ferrets.

Ferrets are generally regarded as nocturnal (Lavers and Clapperton 1990; Alterio and Moller 1997a), but the ferret used in this study showed neither strictly nocturnal, diurnal nor crepuscular activity patterns. Instead, it adhered to an ultradian activity pattern, with many periods of activity interspersed with periods of inactivity. Ferrets, and presumably many other animals, have been labelled nocturnal because they are rarely seen during the day, and mainly seen at night. By using ASTS technology, it was possible to reveal behaviours and activities that may otherwise have gone unnoticed during field observations or when using conventional radio tracking. Therefore, stating that all ferrets are strictly nocturnal is incorrect.

Although the overall activity pattern of the ferret is indicative of an animal exhibiting ultradian behaviour, the daily time budgets generally indicate two main peak periods of activity; one in evening and one in the morning. During the breeding season, the two peaks are quite prominent but during the non-breeding season only one peak period is prominent in the early evening, with a second much smaller period just before sunrise. Otherwise, the main difference between the seasonal time budgets was that the ferret was much more active in total and over over a greater proportion of the day during the breeding season than during the non-breeding season.

Two daily peaks of activity are common in many animals (Aschoff 1966). Several hypotheses for these peaks have been proposed; for example, predators may be: a) attempting to minimise energy expenditure (Weber 1989), b) synchronising their foraging to capture prey (Lodé 1995) or, c) avoiding other dominant predators (Halle 1993). Activity rhythms can also be entrained by physiological endogenous *zeitgebers* to synchronise breeding patterns and body temperature (Aschoff 1964).

Firstly, because mustelids have high metabolic rates, long periods of inactivity may be one way of minimising energy expenditure (Zielinski 1988). For example, stoats (*Mustela erminea*) have a higher metabolic rate than ferrets, but they have a lower energy ceiling that constrains their periods of activity time (Sandell 1989). To avoid exceeding

this survival threshold, they have many short periods of activity interspersed with sleep (King 1989). Although winter temperatures in New Zealand can be cold, they are not as extreme as those experienced by mustelids in their natural habitats in the Northern Hemisphere; therefore, it would be questionable whether the ferret's activity patterns in this study grew out of a need to conserve energy.

Secondly, synchronising their foraging activity to prey activity may stem from the small gut volumes of ferrets. Several peaks of activity may be timed in accordance with both their limited gut capacity and to the periods when prey are available; thus, the activity rhythms of some mustelids may be highly correlated with prey activity (Zielinski *et al.*, 1983; Lodé 1995). The main activity period of the ferret in this study was also similar to that of its main prey, rabbits. Rabbits generally start to appear above ground throughout the afternoon, with virtually all rabbits emerging from their burrows by sunset (Fraser 1992). But this is puzzling; why would the ferret synchronise most of its activity to a time when rabbits are at their most difficult to catch? Surely, it would be more profitable to hunt rabbits during the day when they are confined underground or resting under vegetation.

In a ten year study of rabbits in a 8 ha enclosure, ferrets were only ever observed to chase rabbits above ground on two occasions (Gibb *et al.*, 1978). Although young rabbits can be taken at night while the doe is away feeding, my diet study showed that both adult and young rabbits are consumed (see Chapter 4). Therefore, the question is: when are adult rabbits hunted? Although the ferret in this study was most active after adult rabbit emergence, he was often active underground as much during the day as at night. Wild ferrets may behave in a similar fashion and it may be then that they capture the adult rabbits. ASTS technology may in the future assist in unravelling this mystery.

Thirdly, sleeping to avoid other dominant predators often correlates with the degree of predatory threat (Meddis 1983). Animals that sleep for at least eight hours per day are regarded as good sleepers, while most good sleepers are considered secondary predators that prey upon other species (Allison 1976). For example, secondary predators such as cats (*Felis catus*) are considered good sleepers, spending over 18 hours a day resting (Izawa 1983). As ferrets in New Zealand have virtually no known natural enemies and sleep in well protected dens, they could, in theory, sleep undisturbed for as long as they like; yet, the activity patterns of the ferret in this study contradicted this hypothesis. Instead, it had a polycyclic or an ultradian activity pattern. Additionally, no predators were present inside

the enclosure; however, it is possible that the introduced ferrets of New Zealand maintain an ultradian activity pattern evolved from Europe, where larger predators are common.

Periods of peak activity by the ferret did not always occur at dawn and dusk as one would expect if they have endogenous crepuscular activity rhythms. In November and December (spring), the ferret was as equally active during the day as it was during the night. This conflicts with (Alterio and Moller 1997a) who found ferret activity to be entirely nocturnal in spring. Accordingly, Herrenschmidt (1982) and Lodé (1995) reported that polecats in France were also nocturnal throughout the year. However, mustelids in various other studies, for example, polecats in Switzerland (Weber 1989), stoats in Switzerland (Debrot *et al.*, 1985), and pine martens (*Martes americana*) in California (Zielinski *et al.*, 1983; Debrot *et al.*, 1985), were reported to be diurnal in spring and summer, but switched to being mostly nocturnal in winter. Upon observing similar behaviour for stoats in Sweden, Erlinge (1979) hypothesised that it was mainly transient juveniles which exhibited diurnal behaviour. However, the ferret used in this study was an adult, which suggest that diurnal activity is not always restricted to juveniles. Stockman *et al.*, (1985), researching the effects of oestradiol in ferrets under laboratory conditions, concluded that ferrets lacked a strong circadian activity pattern but did maintain shorter harmonic rhythms between 8-12 hours.

The research mentioned above highlight several inconsistencies in mustelid behavioural activity studies. It is possible that much of this inconsistency relates to the methods used to identify mustelid activity, rather than real behavioural differences. Radio tracking was generally the most commonly used technique to identify ferret activity with radio fixes being obtained at some set interval, normally greater than 10 minutes. The animals were regarded as active if highly erratic signals were produced, and were recorded as inactive if the radio signal was constant (Lodé 1995; Alterio and Moller 1997a). Over a third of all activity bouts by the ferret in this study occurred for less than 10 minutes and most of these bouts occurred during the day. Without this information it is easy to see how a ferret could be regarded as being mainly nocturnal.

For most behaviours, the mean time the ferret took to perform an activity during the day was similar to that at night. The principal difference in the ferret's behaviour, within months, were the number of activities performed during the day compared to the night. For example in June, the **mean time** the ferret *moved* during the day was almost identical to that at night, but the **number of times** the ferret *moved* during the day was significantly

less than at night. Generally, the ferret performed a larger number of activities at night in June (winter) than during the day. This was reversed during November and December (spring-summer) where the number of activities during the day was greater than at night.

However, two points should be made here. Firstly, that the hourly activity rate is dependent upon the length of time the ferret spends performing a behaviour. The number of activities will be low if the ferret spends a long time in one activity such as in *ferret contact* and vice versa if the ferret performs many activities quickly, such as, *drinking* or *digging*. During September the ferret was heard to mate on several occasions during the day; with two mating sessions lasting for more than one hour. In October, the ferret mated with the same female for over an hour on two occasions, once during the day and once at night. Consequently, the activity rate was recorded as low during these times but the ferret was very active.

Secondly, with the day-night cycle changing, the number of day or night activities may also change (Aschoff 1966; Sunquist and Montogomery 1973). This was seen with polecats in Switzerland, where activity was reported to be high, and partly diurnal, in summer and autumn, but mostly nocturnal through the winter (Weber 1989). The day-night cycle of illumination varies in Christchurch from 16 hours of daylight in the summer to 9 hours of daylight in the winter (Land Information New Zealand 1998). When the day-night cycle of illumination was taken into account for each month, the number of activities during daylight hours did not differ from the number of activities during the night.

The ferret ate less often in September and October (the two main breeding months) than in any of the other months studied, and the shortest mean time the ferret took to eat its food was in October. In December, the ferret ate for longer and had more *eating* episodes than any other month and the number of times, as well as the mean length of time, the ferret ate also increased in November. The ferret's weight also showed a corresponding relationship between months (June: 1.624 kg, October: 1.367 kg, December: 1.486 kg). Ferrets and polecats have a marked seasonal variation in body weight with males being the heaviest at the beginning of the breeding season (Danilov and Tumanov 1972; Lavers 1973). The loss of weight in October is probably due to the ferret being preoccupied with breeding rather than *eating* while the increase in ferret *eating* behaviour in November and December is considered an attempt to regain weight lost during the breeding season. This result is interesting as there are two hypotheses concerning food as to why ferrets might be less likely to be trapped during the late winter and spring period.

Firstly, most New Zealand ferret control programmes use rabbit meat to attract ferrets into their traps; however, if ferrets eat less during September and October, then food may not be the best attractant to use as a lure during the breeding season. Ferrets use scent-marking behaviour as a form of inter- and intra-sexual communication (Clapperton 1989) and, instead of using food to entice ferrets into traps during the breeding season, a synthetic scent lure imitating a ferret's presence or another attractant may be a better alternative (Clapperton *et al.,* 1994).

Secondly, it has been suggested that ferrets ignore baited traps in preference to live young lagomorphs. Late winter and spring is also the beginning of the breeding season for rabbits in North Canterbury (Bell 1977), and with such a proliferation of young lagomorphs in their nests ferrets could preferentially hunt these young instead of taking the bait offered. If ferrets do eat less, as suggested by this ferret, then the hypothesis that increased prey availability is the cause for low trapping success may be rejected. However, until further ASTS work is completed, my hypothesis that ferrets ignore baited traps because they are preoccupied with breeding will remain unresolved.

Some captive mustelids will increase their activity if food is given at a particular time, even when the animal is kept in constant darkness (Zielinski 1988). In an attempt to avoid the ferret synchronising itself to any feeding activity in this study, supplementary food was discretely supplied at random. To further reduce the possibility of the ferret entraining itself to any feeding patterns, food was never supplied at the same location, unless the ferrets were to be trapped and in this case the food was placed inside the cage traps. All human activity within or near the enclosure was limited during the recording sessions and was never routine. This was to avoid any perceived predator influence. Therefore, the only exogenous cue for the ferret to set its activity cycle, outside the day-night and temperature cycles, was the remnant population of rabbits within the enclosure. Intriguingly, although these rabbits were present, the ferret was never heard to hunt any of them.

Detecting what an animal is doing underground is a problem. A common assumption is that if an animal is underground then it is probably resting (López-Martín *et al.,* 1992; Ragg 1997). In two New Zealand studies of ferret home range and denning behaviour, ferrets were tracked to their dens with the aid of radio transmitters. Both studies were carried out during the day when they assumed the ferret would be resting (Ragg 1997; Norbury *et al.,* 1998). ASTS results in this study revealed a conflicting story. In many

instances the ferret in this study was just as active underground in its den during the day as it was at night. If a conventional radio transmitter was used to identify the ferret's behaviour, it would be questionable whether many of these activities could be positively identified (Greager *et al.*, 1979). Data from this study indicates that behaviours such as *eating*, *moving* and *female contact* could be frequently heard with ASTS technology when the ferret was underground. This was particularly prevalent in September and October when the ferret was heard to be mating. In the past, ferret mating behaviour has been poorly documented in the wild; however, with the assistance of ASTS technology, future behavioural information on activities normally hidden from view could come to light.

Animals that sleep in well protected burrows are generally regarded as long sleepers and preliminary studies on ferrets found that they spend over 60% of their time asleep (Allison 1976; Marks and Shaffery 1996). Accordingly, the ferret used in this study was observed to sleep for 63% of the time or about 15 hours per day. Ferrets are reported to be polycyclic sleepers, having short periods of waking interspersed with short periods of sleep (Marks and Shaffery 1996). The number of activity/inactivity cycles observed in this study averaged 12 during a 24 hour period and ranged from only a couple of minutes (generally *drinking* or *eating* in between periods of *inactivity*) to several hours duration. The mean time of *inactivity* in October was significantly longer than in August, when the ferret was *moving* around more.

In conclusion, ASTS technology has the potential to unravel many mysteries about animal behaviour and activity patterns. This experimental technique was able to recognise many behaviours that would rarely be identified using conventional observational or radio telemetry techniques. However, as only one animal was used in this experiment, it would be wrong to suggest that all ferrets behave this way until further replicated work has been performed. Thus, a cautionary note must be issued on the weight of the statistical results in this study. No single hypothesis appears to explain why the ferret in this study exhibited an ultradian activity pattern, but it is possible that a combination, or all of the hypotheses discussed, may be operating. Indeed, it may even be a new component that has not been considered before, perhaps future ASTS work will resolve this. Nevertheless, it can be concluded that from the ultradian activity pattern observed in this ferret, it is questionable whether ferrets are strictly nocturnal animals. Finally, from a management perspective, if the aim of a trapping programme is to reduce ferret numbers, then using food as a lure to trap ferrets may not be very effective. Synthetic lures which entice ferrets into traps may be

a better alternative during the breeding season, however, once again, this remains to be tested.

General Discussion

Since ferrets were released into New Zealand over a hundred years ago, opinion on the wisdom of this introduction has remained divided. While some farmers saw ferrets as allies to limiting rabbit numbers, conservationists saw them as a major threat to native fauna. However, by 1995 it was confirmed that ferrets posed an additional threat to New Zealand's dairy, cattle and venison industry as Tb hosts. As a result, investigating behavioural and ecological aspects of ferrets has become vital in understanding the role ferrets play in the spread of Tb. The research outlined in my thesis was tied into a broader study undertaken in North Canterbury, investigating the effects of ferret control on cattle reactor incidence, ferret Tb prevalence, and rabbit numbers (Caley *et al.,* 1998).

The primary objective of my thesis was to monitor natural fluctuations in lagomorphs (rabbit and hare) and predators (cat and ferret) on a non-treatment site in comparison with a treatment site. While predators on the non-treatment site were tagged and then released in a capture-recapture experiment, predators on the treatment site were removed to assess the impact removal had on prey numbers. By monitoring predators using traps, I was not only able to estimate several movement parameters, I also obtained scats for a comprehensive diet study. However, the natural behaviour of ferrets is difficult to observe; therefore, gathering information on their behavioural ecology involves a substantial investment in time, money and technology. Thus, the second objective of my thesis was to examine the natural behaviour of ferrets using an acoustically sensitive transmitter system (ASTS). To date, acoustic studies have been limited to recording a species' vocal repertoire, especially those of birds, cetaceans and primates, but no-one has yet used the sounds created by an animal to build an accurate record of their behaviour and activity pattern. By using the ASTS system, I was able to match a library of sounds and vocalisations to a set of common behaviours and activities analysed from both video and audio recordings of a collared ferret in a small purpose-built enclosure. With this library, I was then able to match sounds and vocalisations recorded in a larger semi-natural study site; and thereby, better understand the natural behaviour of ferrets in the wild.

7.1. Predator/prey population fluctuations

Robust abundance and survival estimates have rarely been reported for ferrets in New Zealand. Although capture-recapture trapping is expensive and time-consuming, it is still the most reliable, versatile and effective method of obtaining ecological information about feral

ferrets (Cross *et al.*, 1998). One of the key assumptions in CR studies is that animals do not lose their tags (Pollock *et al.*, 1990). To test this assumption I compared passive integrated transponder (PIT) tags with ear tags to evaluate the performance of each tagging system. PIT tags were found to be more reliable, more precise and more accurate than ear tags; however, elimination of this bias comes at a cost, as PITs are considerably more expensive than ear tags. Although the survival estimates using ear tags were less precise than those found using PIT tags, they only produced abundance estimates with a negligible loss in accuracy. Therefore, until PIT tags come down in price, the small amount of bias introduced by ear tags may be acceptable. Nevertheless, in this study, all survival and abundance estimates were gathered using the less biased PIT tags.

Most ferrets were trapped in the summer to autumn period, after young had been recruited into the population. Ferret abundance and capture probabilities remained high until mid-winter, but subsequently declined and remained low throughout the spring. Differential capture rates of ferrets between seasons were also reported by Ragg (1997) and Caley *et al.*, (1998). The two main factors hypothesised for a marked variation in seasonal trap success are considered to be both the behavioural differences in trappability and differences in abundance, but I could not distinguish between them.

Animals are not normally distributed at random across the landscape (Perry 1995). Using a completely randomised design to place traps can be wasteful, as some traps will catch many animals, while others will catch only a few or no animals at all. One suggestion is that instead of using a systematic trapping layout as I did, a randomised block design where key habitat features are identified could be more successful. Most ferrets in this study were captured near gullies with plenty of vegetation cover, as well as along animal paths, and while rabbit sign, particularly new burrows and scrapings, was also important, it was often not associated with any one particular type of habitat. Ragg (1997), while identifying many of the same key habitats and features, also found that ferrets concentrated their activity in grazed areas with herbs and scrub present as well as along fencelines. Therefore, identifying key habitat features in a randomised block design could have been used in this study to greater success.

Young male ferrets can be incredibly mobile at certain times of the year (i.e. when dispersing from their natal area and when searching for mates). In contrast, female ferrets limit their movements to generally smaller areas, while maintaining a stronger site fidelity than males. It was found that female ferrets also had a better homing ability than males. Site

fidelity and the homing ability of ferrets has to my knowledge never been tested before and this information in combination with the other movement parameters raises some interesting questions for farmers wanting to control the spread of Tb: if Tb is not present in the livestock, yet ferrets are known to exist in the area, should a farmer remove the ferrets because of their potential to spread Tb? The removal of a stable population of ferrets could create a sink where other ferrets, possibly infected with Tb, could move into the area and infect livestock. Continual trapping may reduce this possibility; nevertheless, Caley *et al.*, (1998) found even intensive trapping over four years on two properties did not reduce ferret numbers significantly.

Intrasexual territoriality occurs when members of the same sex exclude each other from a specific territory (Powell 1993); however, territorial exclusion did not appear to be occurring in North Canterbury. It was found that different ferrets of the same sex would often be captured in the same trap on many consecutive nights. If intrasexual territoriality were occurring, it is doubtful whether so many different ferrets would have been caught in the same trap so close together in time. Nevertheless, it is thought that when prey densities are high, intrasexual territoriality can break down (Powell 1994). For example, Ragg (1997) and Norbury *et al.*, (1998) found that their radio-tracked ferrets in Otago displayed non-territorial behaviour similar to those found in North Canterbury.

Lagomorphs also play a major role in the distribution and diet of ferrets, so much so, that the distribution of ferrets is strongly associated with that of rabbits (Gibb and Williams 1994). Indeed, when rabbits were controlled in New Zealand during the twelve years prior to 1963, ferret numbers also declined (Marshall 1963). Thus, the ferret's reliance on lagomorphs has a major impact on the trapping success of ferrets. For example, when lagomorph densities were low, ferrets were scattered over a wide area; however, when lagomorph densities increased, ferrets moved into smaller patches. Therefore, when setting traps to target ferrets, lagomorph density should also be considered; if lagomorph density is low, traps should also be spaced further apart to match the dispersal of ferrets, and vice versa when lagomorph density is high.

Lagomorph numbers increased substantially on both the non-treatment site, where no predators were removed, as well as on treatment site, where cats and ferrets were removed. As the rate of increase in lagomorphs was similar on both sites, I concluded that the removal of predators (ferrets and cats) did not cause the large increase in lagomorphs. Furthermore, the

dramatic increase in lagomorph numbers also suggested that the normal complement of resident predators could not keep the lagomorph population at a level below carrying capacity.

The greatest increase in lagomorphs occurred in the spring of 1996 at a time when ferret trapping success was at its lowest. One hypothesis for the lack of trap success in spring, was the abundance of young rabbits, resulting in a lack of interest in baited traps by ferrets (Moller *et al.*, 1996). Thus, a low catch rate is believed to be a behavioural response by the ferrets to lagomorph abundance. However, ferret numbers were also low during this period. This suggests that a low trap success rate during the winter to spring period is probably a combination of both low ferret abundance as well as the abundance of young lagomorphs. If trap success is related to the plentiful supply of particularly young rabbits, it could also be hypothesised that ignoring baited traps would continue until there were fewer young lagomorphs available. However, during the summer to autumn period, many ferrets were captured in spite of the fact that a high number of young lagomorphs were still available. This suggests future trapping programmes need to consider both seasonal affects and availability of young lagomorphs when targeting ferrets for control.

7.2. Comparing predator diets

Compared to polecats in Europe, ferrets in New Zealand have a narrower diet, although they are not considered true specialists. It has been argued that their narrow diet here, is due to the lack of suitable alternative prey. Over 70% of ferret diet is lagomorph, with birds, rodents, reptiles, invertebrates and carrion completing the remaining 30%. In comparison, polecats in Europe target anurans and rodents as their main prey (58%) (Brugge 1977; Sidorovich and Pikulik 1997; Weber 1989), while eating a greater variety of alternative prey (42%) than ferrets in New Zealand (Lodé 1997).

Although not as dependent on lagomorphs as ferrets, feral cats in mainland New Zealand also consume quite a narrow range of prey. In North Canterbury, cat diet was virtually the same as ferret and, again, this is attributed to the lack of suitable alternative prey. The diet of cats found on islands, where there are fewer small mammals available, is ever narrower than those found on mainland New Zealand. However, cats in Australia generally have a greater diversity of prey available and, as a result, their diet is more generalised than cats in New Zealand.

As already stated, ferrets have such an exceptionally strong relationship with lagomorphs, their diet and distribution in New Zealand are invariably linked. Because of this,

one possible means of reducing ferret numbers is to concurrently reduce lagomorph numbers. Indeed, Norbury *et al.*, (1998) demonstrated that a reduction in lagomorphs significantly reduced the recruitment rate of ferrets. Unfortunately, they also found that the surviving ferrets increased their movements, possibly posing a further risk to managing Tb. An additional problem in reducing lagomorph numbers, is a short-term increase in ferret predation on native fauna (Norbury and Heyward 1997). Therefore, to better understand the relationship between lagomorph numbers and ferret abundance, further studies are needed to address the long-term impact of ferrets predation on alternative prey when lagomorph numbers are low.

7.3. Documenting ferret behaviour using an acoustically sensitive transmitter system

Although conventional radio tracking has unravelled many ecological and behavioural aspects of animals, observing their natural behaviour in the wild can still be extremely difficult (Mech 1983). Chapter 5 was dedicated to testing a complimentary methodology to conventional radio tracking, that would allow a researcher to locate an animal and then study its natural behaviour without disturbing it. Chapter 6 measured the activity patterns and behaviour of a male ferret during the breeding season using an acoustically sensitive transmitter system (ASTS).

One approach to monitoring the behaviour of an animal without disturbing it, is to use ASTS equipment to record the sounds and vocalisations associated with certain behaviours. By using ASTS technology I was able to identify: a) when the ferret was active; b) how long individual behaviours occurred; and c) the frequency and sequence of behavioural events. More importantly, I was able to identify some important behaviours such as *eating, drinking, grooming, digging* and *female* or *male contact* which may often not be identified either using direct observations or with conventional radio tracking.

Low trap success during the winter to spring period has major implications for ferret control programmes. Behavioural aspects, such as a ferret's preoccupation with breeding, as well as their mode of feeding, may both help explain why few ferrets are captured during the winter to spring period (Moller *et al.*, 1996). However, analysing behavioural reasons for low trap success is hampered by current technology. Therefore, the primary reason I used the ASTS technology was to explore current hypotheses put forward concerning the natural behaviour of a ferret over the breeding season.

Several interesting findings became apparent during this study. Firstly, the ferret was often almost as active during the day as at night; nevertheless, most diurnal behaviour (i.e., *ferret contact, eating, digging, moving* and *active*) occurred when the ferret was underground. Therefore, stating that ferrets are nocturnal is incorrect. Secondly, the ferret displayed an ultradian activity pattern, with many short periods of activity, rather than a single period of activity at night or two periods of activity that peaked in the early morning and evening. Finally, the ferret ate significantly less during the breeding season (mainly September and October), which could explain why fewer ferrets are caught in baited traps. Another hypothesis for the low trap success in the late winter and spring, is that ferrets preferentially hunt the newly born lagomorphs in their nests rather than take bait set in traps. However, if ferrets do eat less because they may be preoccupied with breeding then this hypothesis would be invalidated. But as only one ferret in a large enclosure was recorded in this study, these results are only *suggestive* of what ferrets may do in the wild.

ASTS technology does, however, have certain limitations. Firstly, the size of the battery determines the recording time, and if the animal is small it can only carry a small battery, thus, the recording time will be short. Secondly, for animals that frequent subterranean habitats, it is possible that the audio signal will be lost if the animal goes deep underground. Thirdly, in using ASTS collars, there is an additional cost for recording equipment not normally used in conventional radio tracking. Finally, the signal range can occasionally be more limiting that than used in conventional radio tracking systems because the audio signal is much more sensitive. However, once an animal has been located using a conventional radio tracking system, a researcher using ASTS equipment can move into audio range without ever seeing or disturbing the study animal and listen to its behavioural sounds.

7.4. Future work

7.4.1. Questions raised

Trapping success of ferrets (as well as cats) is extremely variable, both temporally and spatially. Various hypotheses for this variance in trappability have been investigated and discussed in this study; however, there are still many questions yet to be answered:

1) ***What are the agents that cause ferrets to decline before the late winter to early summer period?*** Trap-catch rates have been found to be very low from late winter to early summer

and low ferret abundance is hypothesised to be one contributing factor. A study of known aged ferrets wearing mortality sensors could answer this question.

2) ***Do predators hunt young lagomorphs in preference to an easy meal of lagomorph bait and, why does this preference appear to be only a seasonal phenomenon?*** With a good supply of bait available why do the ferrets seemingly avoid traps? Increased prey abundance in the form of young lagomorphs is hypothesised to be one explanation as to why it is difficult to trap ferrets from late winter to early summer. But if this is true why are we able to trap relatively more ferrets in late summer and autumn than in late winter and early summer when there are still plenty of young lagomorphs present? Feeding experiments using a variety of prey types and sizes could help answer these questions while also addressing questions on the optimal foraging behaviour of ferrets.
3) ***What are the other key factors that influence trap success?*** Often, when using a systematic or simple random design, some trap sites will be extremely successful while others will catch nothing. Therefore, it is imperative to identify the main factors that contribute to a trap's success or failure. Once identified, these factors can then be allocated into a stratified random design to specifically target ferrets.
4) ***Do new or transient ferrets move into areas (sinks) after the original ferret population has been removed?*** One of the concerns of farmers about the ferret's role in spreading Tb, is the consequent effect of eradicating current ferret populations. If re-invasion occurs, then re-invasion rate models need to be developed for assessing the epidemiology of Tb in New Zealand.
5) ***Would continually keeping lagomorph numbers low actually reduce predator numbers?*** Lagomorphs are the primary prey of ferrets and cats in New Zealand and their numbers strongly influence predator numbers. Theoretically, predator numbers should decline after lagomorphs numbers are reduced, but if long term prey switching is sustainable, then predator numbers may remain relatively high at the expense of some other, possibly endangered, prey species. Only a long-term study will be able to address this issue.
6) ***Would leaving a resident population of cats in an area where ferrets have been removed assist in keeping rat and stoat numbers down?*** Tb prevalence in cats is much lower than in ferrets and if both cats and ferrets are removed then it is possible that rat and stoat numbers could increase. Both rats and stoats are considered by some to be more detrimental to wildlife than cats. However, this strategy should only be tried in areas where no endangered wildlife are present.

7) ***Are ferrets only nocturnal?*** I found that the ferret in this study exhibited an ultradian activity pattern which suggests that ferrets are not nocturnal, but until my work is replicated using multiple subjects this question will remain unanswered.
8) ***How are animal activity patterns assigned?*** One method to deduce animal activity patterns has been to use variations in radio signals. Differentiating between some radio signals can be extremely difficult, especially if the animal does not physically move from one location to another. Therefore, questions about the accuracy of using conventional radio tracking signal to describe an activity pattern need to be raised.
9) ***Do ferrets eat less during the breeding season?*** The ferret in this study ate less during the two main breeding months than in any other month recorded. If ferrets eat less, and eat less often during the breeding season, this could explain low trap success during these months. Although, the information developed from feeding trials suggested in question 2 will be useful, another suggestion is to trial synthetic lures made of male and female pheromones, instead of baiting traps with rabbit. This may result in improved capture rates over the breeding season.
10) ***Do ferrets perform the same vocalisations throughout the year, and how do vocalisations vary when near conspecifics?*** Although not explored in this thesis, there is a myriad of questions that could be asked using additional vocalisation information gathered during my research.

7.4.2. Further work and recommendations

1. In long-term studies, greater than two years, PIT tags have been found to be both more accurate, as well as less biased, than ear tags. Although PIT tags cost substantially more, their longevity and accuracy could be worth the investment. However, over the short-term, the benefits do not outweigh the costs; therefore, ear tags are recommended even though a small loss in precision may result.
2. A similar capture-recapture study with spotlight counts should be performed to monitor and compare the natural fluctuations of predators and lagomorphs at a time when lagomorph numbers are relatively low and stable. Additionally, instead of only one non-treatment and treatment site, there should be at least a minimum of two non-treatment and treatment sites sufficiently apart.
3. ASTS collars, in combination with conventional radio tracking systems, should be tested on feral ferrets, or other suitable animals, in the wild. Although the system worked well

while the ferrets were enclosed, the ultimate test of the ASTS technology would be on a free-ranging ferret. Ideally, the test should be performed using a team of people following the activities of a resident ferret. This way the ferret can be recaptured and the ASTS collar returned. In addition, instead of using standard audio tape, a portable digital audio tape (DAT) recorder, would be preferable because; a) the signal is digitised, b) the recorders are small and lightweight and, c) they can record for a greater period of time than a standard audio tape recorder.

4. The most time-consuming demand on the ASTS study was listening to the many hours of video tape. Once the behavioural sounds of an animal have been digitised and organised as a library of sounds, a computer algorithm could be constructed to identify individual behaviours when they occurred. This would substantially reduce the analysis time.

7.5. Concluding remarks

This thesis was divided into two main sections: a field study and a captive study. The field study used a variety of conventional methodologies to address ecological and behavioural questions, whereas, the captive study used a novel approach to studying ferret behaviour. Although a variety of aspects of the ecology and behaviour of ferrets were examined, my study highlights that there is still much to be learnt. As a result of their elusive and shy nature, ferrets are not easy to study, and anyone researching mustelids, or any elusive animals, will be familiar with the problems associated with studying difficult animals. Nevertheless, this makes the challenge all the more worthwhile and rewarding.

While there is no doubt that this study provided some new behavioural and ecological information on ferrets and supported several hypotheses proposed, the ASTS work probably provided more questions than answers; however, it was successful in examining a methodology that could, in the future, be used to answer many questions on the behaviour and ecology of ferrets, or indeed on many other animals.

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